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FISHERIES HYDROGRAPHY

Introduction.

By

C. E. Lucas

In 1949, the late Dr. R. S. Clark proposed that the Council should take an early opportunity to discuss the place of hydrography in fisheries research. Following upon the submission of several papers[1]) on this subject to the Northern North Sea Committee in 1950, and with the strong support of the President[2]), the Council decided to arrange a Special Scientific Meeting for the purpose during the Amsterdam Meeting in 1951. Dr. Lucas was appointed Convener and Dr. Poulsen, Reporter.

The meeting was held in the Museum of the East Indies on Saturday, 6th October, beginning at 9.30 a.m. Nearly all the papers had been prepared and circulated in advance, so that the contributors were required merely to give brief accounts of their papers so that a discussion could follow. After a few remarks by the Chairman elected for the meeting (Dr. Lucas), who referred to the great practical importance of the subject, Professor H. U. Sverdrup opened the session by giving the views of a professional hydrographer on the place of hydrography in fisheries investigations. Among other matters, he emphasised that it is the task of the biologist to demonstrate the reactions of the fish towards different types of environment. In the light of this knowledge the hydrographer should study the *processes* by which the environment is *changed*, as well as its momentary condition, so as to be in a position to *forecast* hydrographic situations of fisheries significance. In particular he made a plea for the hydrographer and the biologist to meet daily and to learn to write and speak so that each understands the other, as well as to disseminate their information speedily.

Professor Sverdrup was followed by Dr. H. O. Bull who had been specially invited by the Council to address the meeting on fish behaviour in relation to specific hydrographic characters. After defining the problem and reviewing our present knowledge of individual and mass behaviour in fishes, Dr. Bull went on to give a valuable account (by special request) of his own methods and contributions in the field of conditioned responses. He then posed to the meeting a number of questions, together with such answers as the present state of experimental research permitted (p. 22). It was particularly significant that research had shown the ability of "conditioned" fish to discriminate between salinity, temperature and pH values almost as finely separated as those our present hydrographical analyses can distinguish. The natural distribution of these factors therefore provides a possible system of "directive" stimuli. Finally, he made an appeal for the preparation of monographs, based on observation and experiment, of the *normal* behaviour of fish, particularly the fish of commercial importance[1]).

The subsequent fourteen papers ranged over a wide field, and may be grouped roughly as follows:—

Miss E. Henly first described some very interesting

[1]) Of these the following have been published in the same or a similar form:—

Carruthers, J. N., Lawford, A. L., and Veley, V. F. C. Fishery Hydrography: Brood-strength fluctuations in various North Sea fish, with suggested methods of prediction. Kieler Meeresforsch., Bd. 8, Heft 1, pp. 5—15, 1951.

Carruthers, J. N., Lawford, A. L., Veley, V. F. C., and Parrish, B. B. Variations in brood-strength in the North Sea haddock, in the light of relevant wind conditions. Nature, Lond., Vol. 168, pp. 317—319, 1951.

Tait, J. B. On the Application to Marine Research of the Meteorological Concept of Accumulated Temperature. Journ. du Cons., Cons. Int. Explor. Mer., Vol. 17, No. 2, pp. 111—120, 1951.

[2]) Andersson, K. A. Co-operation between Biologists and Hydrographers. Rapp. et Proc.-Verb., Cons. Int. Explor. Mer., Vol. 129, I, pp. 29—32, 1951.

[1]) It should be recorded here that Dr. Bull has added to the debt incurred by fisheries workers in bringing up to date the bibliography begun by him in collaboration with Dr. E. S. Russell in 1932. This will be published in the Council's Journal.

observations on conditions leading to heavy mortality of various fish larvae (chiefly cod). Experimental results suggested to her that high oxygen tension might have a harmful effect, whilst in general sudden changes in water pressure led to a heavy mortality with associated signs of "gas disease".

Mr. F. S. Russell provided an invaluable review of plankton research in relation to hydrography and the fisheries (with full bibliography). He concluded this by making a special appeal for correlations between the survival of fish year-classes over a long period and the abundance of associated plankton organisms during their pelagic stage, particularly those which may be vital sources of food at a critical stage.

Dr. J. H. Fraser's paper gave a more detailed consideration of plankton in relation to the hydrography of the northern North Sea, with particular reference to the Chaetognatha as "indicators" of water types of hydrographical and biological significance.

Dr. D. J. Rochford (Australian observer) introduced a very different aspect in his account of an attempt to increase the food supply over the oyster beds in a relatively barren Australian estuary. This was achieved experimentally by increasing the nutrient content of the intertidal mud, apparently with subsequent increase of the surface film of microorganisms and resultant detritus.

Looking at the problem from the more hydrographical viewpoint, Dr. L. H. N. Cooper briefly reviewed his recent work on "cascading" and "capsizing" phenomena off the west coasts of the British Isles. He outlined the possible ways in which these processes might influence the biological cycle in their neighbourhood, particularly (he thought) by leading to extensive local concentrations of zooplankton which directly or indirectly might induce local concentrations of commercial and other fish.

Dr. Aage J. C. Jensen and Dr. H. Alander, from different points of view, then reviewed the extensive data accumulated by various workers on associations between the sharp hydrographic boundaries and the variations met regularly in the Baltic and the Transition Area and the varying success of the local fish, their eggs and larvae, and the commercial fisheries.

Both called for more intensive observation in this field and Dr. Jensen in particular for more precise determination of hydrographical changes. Their papers were followed by one from Instr. Lt. V. F. C. Veley, providing a further example of changes in the success of a fishery (this time of the sprat fishery, both off the East Anglian coast of England and off the west coast of Sweden), apparently associated with changes in wind strength and direction around the time of hatching and early larval growth. He emphasised that the data only pointed to the *possibility* of such an association, although it seemed to him very significant that the data from the two fishing grounds responded similarly to identical analytical treatment. Whilst these various observations point as yet only to "associated" phenomena, it may be difficult to resist the view that in some instances the workers have been discussing relationships which may come to be seen as "cause and effect".

In a quite different field, Dr. H. Einarsson discussed some instances of parallelism between the success of the summer and the following spring spawning herring broods in Icelandic waters. He considered these to imply that "external" factors must remain reasonably similar from July of one year to April of the next, whereas they must be expected to have changed before the following February. He was able to demonstrate that major hydrographic and planktonic changes may indeed occur at that season and he hopes to collect further evidence on these points.

Four papers then followed, all indicating in one aspect or another an "operational research" approach, i. e., one in which the problem is met fairly and squarely in the field, with hydrographers and biologists working together to relate the distribution of the fish as caught or observed to their immediate environment at the moment. Mr. R. E. Craig's paper could merely refer to the first season's work on the Scottish East Coast herring stocks, with comments on some interim results. Dr. L. A. Walford (U. S. observer) gave a very interesting account of the large scale U. S. investigations of the environment of the Californian sardine and the Pacific tunas. The former have already indicated that spawning is confined to the temperature range 12.5°—16° C., and the latter that fishing for tuna may be more successful along the Pacific equatorial divergence than elsewhere.

Mr. F. Devold was able to continue his earlier tracing with the "G. O. Sars" of the apparently hydrographically directed course of Atlanto-Scandian herring shoals from Iceland to Norway by showing something of their return route with indications of the associated hydrographic determinants. Mr. A. J. Lee followed by giving a preliminary account of the work of the "Ernest Holt" off Bear Island and in the Barents Sea on the apparent impounding of cod in hydrographic pockets under certain conditions. Whereas Mr. Devold found the herring to be limited to the deeper cooler Arctic water in the winter and to rise into the warmer surface water as summer arrived, Mr. Lee and his colleagues found the cod to have one temperature preferendum (1.75°—3.00° C.) to the south of Bear Island and another (3°—5° C.) to the west. Mr. Lee emphasised the necessarily tentative nature of these associations at present whilst showing how fishing by their guidance would have led, and at times had led, to large catches.

Dr. G. Böhnecke (German observer) gave an account of the reorganisation of fisheries research in Germany after the war, in particular outlining hydrographic and related developments. The latter included special studies of the thermocline in the Northern North Sea and its influence on the fisheries, and detailed studies of current variations in the

Southern North Sea (in conjunction with Netherlands and British workers).

After some discussion the following resolutions were transmitted to the Consultative Committee and were ultimately approved by the Council.

The sincere appreciation of the meeting was expressed by the Chairman to Dr. BULL and the other contributors for their stimulating papers, this appreciation being subsequently endorsed by the Council in General Meeting.

Recommendations as amended by the Consultative Committee.

1) As the proceedings of this meeting have shown that a combination of biological, hydrographical, meteorological, physiological or statistical researches has furthered our knowledge of biological productivity, of the habits of the fish stocks, and also the fisheries themselves, it is recommended that researches along these lines should be continued.

2) It is recommended that committees should state as definitely as possible what problems they wish the hydrographers to attack and solve.

3) It is recommended that compendious studies of the normal behaviour of our major food fishes should be carried out either by direct observations or by laboratory experiments.

4) It is recommended that efforts should be made to encourage the writing of monographs describing the hydrographic conditions in the seas in which fishery research workers are interested.

5) It is recommended that as a direct means of showing the dependence of the fish stocks on hydrographic conditions, and as a direct help to the fisheries, experimental fishing on a commercial scale and other forms of assessment should be carried out simultaneously with hydrographic observations.

6) It is recommended that the immediate aims of the Plankton Committee should include (i) studies of the basic conditions of productivity in the sea, and (ii) an attempt, by observations over a series of years, to correlate the number of survivors of a year-class of fish with the presence or absence of any one or more types of plankton organisms, both predatory and food-producing, during the early planktonic life of the fish.

7) It is recommended that the contributions to this meeting be published by the Council as a special report. Contributions that are or will be published elsewhere should only be abstracted in the report.

8) It is recommended that the results for cod near Bear Island and for herring in the open Norwegian Sea be brought to the attention of the fishermen of all countries.

A. For cod fishing near Bear Island.

(i) That on grounds west of Bear Island, in early summer and again in autumn, atlantic type water touching the bank can give good trawl catches, with bottom temperature near $3^3/_4°$ C.

(ii) That west of Longitude 20° E. a bottom temperature of less than $1^3/_4°$ C. is generally unfavourable, and so may cause concentrations of cod near its boundary.

B. For herring in the Norwegian Sea.

During the last 4 years (1948—1951) herring shoals have been observed in extensive areas over the deep water north and north-east of the Faroe Isles in May-June.

Later in the summer the shoals seem to concentrate in the border region of the East Icelandic Arctic current between 66° N. Lat. and Jan Mayen. In the two recent summers the Norwegian investigations have shown that the herring shoals are also numerous from Jan Mayen north-estwards along the border between the atlantic and the arctic water, temperature approximately 6—8° C. in the open sea.

Last summer (1951) herring drifters made good catches 80—100 n.m. east of Langanes, Iceland, and also in the Jan Mayen area.

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1.

Some Remarks on the Place of Hydrography in Fisheries Research.

By

H. U. Sverdrup

When speaking of the rôle of hydrography in fisheries research it is inevitable that trivial statements are repeated, but some of these can stand repetition.

We may, I believe, all agree that the most important goal of fisheries research is to prepare predictions of value in fisheries problems. The question before us today may, therefore, be formulated as follows: How can hydrography assist in preparing predictions?

Generalizing it may be stated that the predictions to which hydrography can contribute fall in two groups, the prediction of availability and the prediction of the size of the stock.

When one considers prediction of availability, the first step is to ascertain if a given species of fish may be caught commercially within specific hydrographic conditions. If so, the next and much more difficult step is to predict when and where such hydrographic conditions can be expected to occur. At the first step biologists and hydrographers must co-operate. At the second step the hydrographers are on their own, but when presenting their conclusions they must use a language less technical than that they can employ among themselves. There exist examples of successful predictions, but I believe it should be borne in mind that one cannot expect exact conclusions; one has to be satisfied with the prediction of probabilities because, even if the hydrographic conditions could be predicted exactly, these alone do not always determine the presence or absence of fish.

Knowledge of the hydrography may lead to predictions as to the size of the stock if the hydrographic conditions are of particular importance at one stage of the development of the species. As an example the recent work of Carruthers, Lawford & Veley may be mentioned. For a number of North Sea fishes the authors assume that the direction of the currents during and shortly after the spawning period is important to the success of the spawning, because the currents may carry the fish larvae into regions where food and other factors are favourable or unfavourable. Lacking information as to the currents, they have used the wind as an indicator and have obtained remarkable correlations.

In this case knowledge of the hydrography has found a direct application, but in many other instances such knowledge must be used in conjunction with many other types of information. This is the case if one wishes to base the prediction on a complete understanding of the complicated sequences of events that take place from the time of spawning and until the fish can be caught commercially. When dealing with this chain of events knowledge of the hydrography is of immediate importance when considering the primary production of organic matter in the sea and it enters at every subsequent stage. The hydrographers and the biologists have at all times to co-operate, but the success of co-operation will to a great extent depend upon the mutual understanding of their respective problems.

Among the types of predictions related to the size of the stock I also wish to include prediction as to the effects of overfishing. In this case knowledge of the relationship of the species of fish in question to its environment seems indispensable if it is to be possible to recommend adequate measures of preservation.

The line of inquiry which aims towards a complete understanding of events necessitates such a variety of investigations that they cannot all be undertaken by the fisheries research laboratories, but fortunately the International Council has its roots among the numerous laboratories of other organisations and draws many of its members from these. Bearing in mind its distant goal the International Council should, therefore, be able to exercise an influence on the trend of marine research, impulses should go out from here and our activity should benefit from impulses received from other workers in adjacent fields. In all this work hydrography will not assume a unique position, but must take its place as an integral and indispensible part of the combined effort.

2.

An Evaluation of our Knowledge of Fish Behaviour in Relation to Hydrography.

By

H. O. Bull

I. Introduction.

Many of the scientists here gathered together, as well as those who have met in the same way during the past fifty years are for the most part, naturalists of the high seas, followers of the movements of vast masses of water, or dealers in the broad sweep of statistics. By contrast, much of what I have to say belongs to the very tiny world of single small fishes (or even little bits of them) in small experimental tanks. It will be for you to consider when I have finished whether the two have anything in common.

It has indeed been a feature of the work of the Council that it has concerned itself largely with the activities of men, machines, and methods used in catching fish in the mass; or with the impersonal properties of the worlds in which fish live; or the lifeless attributes of fish populations, rather than with the behavioural characteristics of the fish themselves. This latter work has been left largely to the whim of private investigators either in the Universities or in the non-Governmental laboratories. Nor is there much evidence that the Council, as a body, has ever seriously considered whether such information is necessary to the carrying out of its duties. Is this not rather like a Steel Founder working without his Metallurgist?

1. Definition of Behaviour in the present Context.

In this context I define Behaviour as the sum-total of the receptive, perceptive, and reactive capacities and activities of fish in so far as they can be observed and recorded; if there are any other aspects of these activities then, even if they exist, we cannot be said to have real knowledge of them and must here ignore them. Not every student of behaviour would agree to this definition.

All animal, including fish, behaviour whether it be 'privately known', subjective, and externally non-observable—or 'public' and objectively observable, may be broken down for scientific treatment into three phases:—

1. The initial phase of reception or perception—in which the organ or organisms is put into a state of awareness or 'excitation' in the physiological sense of the word.

2. The intermediate phase or mechanism of co-ordination whereby the 'excitation' is transmitted from the site of stimulation to the region where the response is carried into effect, and

3. The observed phenomena of behaviour as shown in the carrying out of the appropriate response either of the whole or part.

Under each of these phases we have also to consider the findings of other specialised branches of biological science. Thus we have to know what is going on with the chemistry and physics of interfaces, the structure and behaviour of receptor surfaces, and the properties of specialised receptors. Although fish have a large number of known or supposed receptors, some e. g. the lateral-line sense organs and the organs of posture and equilibrium have received perhaps disproportionate attention; and many none at all.

Under phase 2 we must keep in touch with what is being done in nerve and sense physiology generally as well as with fish; the electro-physiologists have made notable and valuable contributions in recent years to our knowledge of the relation between fish and their environment.

In phase 3 we have again the same general kinds of problems relating to effectors as with receptors, except that they are perhaps even more varied—muscular or ciliary movement, elaboration of secretions, production of noise, light, electric discharge, change in body colour, etc.—the kinds of things more generally thought of as 'Behaviour'.

Practically, these specialised aspects resolve themselves into four more or less distinct disciplines, into one of which research usually tends to fall. These are:

1. The consideration of the mechanisms available, treated morphologically as forms and structures, e.g. Herrick (19) on Menidia.

2. The same, treated dynamically as working machinery, e. g. Hoagland (20) and Adrian (1) on nerve impulses from sensory endings.

3. The effect of internal or external secretions, in so far as they affect the total pattern of behaviour (in the strict sense these arise out of 1 and 2, but there is a practical value in keeping them distinct) e. g. the work of Fontaine (14), of Noble, Kumpf, and Billings (25 a).

4. The consideration of the finalised patterns evolved in total behaviour by these basic mechanisms; and the effect upon them of development, circumstance, accident, disease, heredity, sexual state, etc.

It is obvious that we shall look at these different separate problems from different angles, according to our bent, so that many kinds of attack on the fundamental problems of fish behaviour are in fact possible and profitable. It is, I think, retarding to progress to restrict consideration, as many students of behaviour do, to any one of them; and much worse, positively to exclude them.

The same general attitude should prevail in regard to field versus laboratory studies. Much description of behaviour 'in the field' is anecdotal and not very critical; yet good field work is rapidly becoming more and more experimental in the sense of being a controlled study with all the relevant factors properly assessed. On the other hand laboratory work will suffer if the experimenter has not already a wide knowledge of his subject in the field or in a good aquarium.

2. The Extent of present Knowledge.

There are, I think, two main kinds of question which this meeting may reasonably ask the student of fish behaviour, both in respect of individual fish and fish in the mass.

1. Are any features of their normal environment perceived by fish in such a manner as to enable them to make use of them, either voluntarily and intentionally, or involuntarily? if so, are any of them important hydrographically?

2. Are the apparently hereditary behaviour traits of fishes—especially their feeding, shoaling, or migratory movements—determined in any way by measurable properties of the seas and rivers? If so, what are they, and are such hereditary traits modifiable by changes in these properties?

The extent of our knowledge to date on these issues may soon be gauged.

Russell and I (29), in 1932, listed together in a convenient form all papers then known concerning fish behaviour, subject to some qualification. Thus, we excluded purely physiological papers, papers relating to fishery investigations, and observations on special habits. Our object was to include all experimental work which had appeared up to the end of 1931. The work involved was considerable, since the literature was very scattered, and much of it in journals then mostly unknown to the general zoologist. Shortly before that date however, Biological and Psychological Abstracts both started publication; together with Physiological Abstracts, and the Zoological Record, the Bibliographia Oceanographica, and of course your own Journal du Conseil, these make such a task to-day comparatively easy. Nonethe-less I have continued our bibliography of Fish Behaviour down to the present time and intend to submit it as a continuation of our joint effort to the Editor of the "Journal" early in 1952. It will thus cover a further twenty years since the last one.

These two bibliographies between them will cover, with the reservations already made, all the literature on fish behaviour in the scientific sense. The original joint paper listed some 700 titles; the one now in MS lists a further 500; it includes however fewer general works, and probably more physiological ones than my former collaborator would be likely to approve—but there are none I think that Psychological Abstracts would not also include.

The analytical treatment of the 1932 paper makes further analysis of it unnecessary here; the MS list, covering the past 20 years, omitting for the moment my own work, shows that, of the total of 500 papers, only approximately $^1/_5$th are devoted to marine fish. Sixteen are about marine fishes generally or some group of them; 19 are about non-European species i. e. *Megalops* (3), *Fundulus* (13), Plectognathidae (1), *Prionotus* (2); and 67 deal with European fish. Five of these relate to 5 fish of no commercial interest, and 62 to those of commercial interest, comprising in some instances more than one species. The balance of the total is given to fresh water fish. Of these *Phoxinus laevis*, *Ameiurus nebulosus* (or other Siluroid), and *Carassius auratus* far outnumber all other species.

It is perhaps unnecessary for me to say that what determines this situation is not the importance of the questions to which an answer is sought experimentally, but the suitability of the species selected for experimental conditions. I have no doubt that if sufficient stress were laid on the importance of working with the major food fishes we should sooner or later find ways and means of keeping them also.

Classifying the papers further by their subject matter, it is found that almost all those referred to as dealing with marine fishes relate to aspects of their behaviour which, however intrinsically interesting and important in themselves can have little value in the present discussion, e. g. colour change, anatomical studies of sense organs, physiology of locomotion, spinal reflexes, observations of aquarium habits, etc. Although the time available to me for preparing this has been short, I do not think I have been guilty of any gross omissions in this analysis, if it is remembered that fishery papers and field observations in general are excluded specifically. In fact, only 6 out of the 62 fall into the last of the four disciplines I

outlined earlier, i. e. 6 deal with behaviour studies, 8 with colour change, 48 with anatomy, physiology of sense organs, locomotion, spinal reflexes etc. Further, not one of the 6 is relevant to this discussion. This shows better than words why it is often difficult, if not impossible, to answer enquiries about the sensitivity of our food fishes to environmental factors. My own experiments have been excluded from this analysis.

If provisional answers are demanded to sensory problems, other than those with which I deal later, we have largely to fall back upon very old work or upon the three well-studied fresh-water species.

3. Methods by which Knowledge of Fish Behaviour has been gained.

It is, I believe, important to you as hydrographic experts—working with the tools of the so-called 'exact' sciences—that you should be able to assess for yourselves, in your own way, the value of the contributions which behaviour studies may have made, or be able to make to your work. I propose therefore to summarize first and briefly, the methods by which such real knowledge as we have has come into being.

A little earlier, I listed the four more or less distinct disciplines into which this work generally falls. The first of these needs only the slightest word. The comparative neurologist and the histologist, using their standard techniques, have made vital contributions to the interpretation of behaviour. Herrick (19) wrote that "Nature has, as it were, performed in fishes a series of experiments which reveal clearly .... the primary and secondary centres for the several systems of the sense organs", and that "we may now associate the several lobes of the *Medulla oblongata* which are so characteristic of fishes with their respective cutaneous or visceral sense organs as definitely as the olfactory nerves are associated with the olfactory lobes ...." etc. He continues that "one of the best illustrations of this central response (i. e. the enlargement of certain regions or lobes of the brain) to peripheral differentiations is found in the sea-robins (*Prionotus*), in which certain free rays of the pectoral fins have become exceedingly sensitive finger-like tactile organs and their sensory nerves, together with the corresponding dorsal horns of the spinal cord, have been in consequence enormously hypertrophied". Scharrer (31), however, says that the free rays are relatively insensitive to tactile stimuli, that if these stimuli are weak they are only effuctual when summated, and that cotton-wool evokes no response unless soaked in meat juice. Several recent workers, e. g. Evans (12) and Bhimachar (4) have continued this excellent mode of approach, yet it is clear that faulty inferences may be drawn. Evidence concerning perception drawn from it can only be inferential.

Precise information about the histology and general morphology of receptors is also important as may be seen from one recent example among many, e. g. Pumphrey's hypothetical deductions (27) based largely upon such data about the sensibility of the *lateralis* system in fishes. How far these deductions may be of real value in this present discussion is hard to say—but he himself says that the silence of the deep waters is a myth, that everything that moves must produce infrasonic noise, and suggests that, for a fish, the increased powers of auditory analysis coupled with the directional possibilities of the *lateralis* system make this system its most likely distance receptory mechanism. If this were proved to be so, it would clearly have to be considered in the present context. Much speculation on sensory capacity has unfortunately been made on the basis of histological and morphological study, yet it must continue to be necessary.

Physiology, and especially electro-physiology of receptor mechanisms and the study of locomotory and spinal reflexes has played a large part in recent work on the relations of fish to their environment, and in the establishment of causal relationships must also obviously continue. I need only mention the very valuable work of Hoagland (20), Sand (30), von Holst (21), Adrian (1), Gray (17, 18), Lowenstein (24), and many others, for it to be certain that here likewise, in spite of many difficulties, they have much to tell us which is important in a right appreciation. The puzzle is how to relate their findings to the intact living fish.

It remains for the fourth discipline to provide the most useful contribution to this discussion. A convenient division is into receptive and reactive capacities. In studying receptive capacities we may distinguish the use in the past of five more or less separate methods, which can be specified in terms of the stimulus conditions, motivation factors, and the nature of the response chosen as giving indication of perception. Two of these are non-training, three of them training, methods.

The non-training methods are the 'preference' and the 'stimulus-test'. In both of these, simple observation only is made of the reaction of the fish to the experimental situation. With the first, this consists of either a pair of unlike stimuli, e.g. an aquarium of which one half is flooded with light of one colour and the other with a different one; or of a gradient of one specific stimulus—to which the degree of selective activity is noted, e. g. Shelford & Allee (32). With the other, the stimulus is applied singly and directly; the activity may be positive-towards, or negative-withdrawal. The observations of Bateson (2) and Scharrer (31), widely separated in time, are typical examples.

The training methods are the 'discrimination-response', the 'conditioned reflex' and the 'complex task'. The first two of these are discussed at a later stage in this paper. The 'complex task' involves the solving of some elementary spatial situation, such as a maze or detour, neither of which, in the case of fish, has yet been made other than quite simple. The fish having 'learnt' the situation changes are made in

the sensory cues at appropriate points. Evidence of receptive discrimination is obtained from the effect of these interpositions on the learned behaviour. Examples are the work of SPOONER (34) and RUSSELL (28). The 'complex task' has also been much used in the study of the second major category of reactive capacities.

It is true of fish, as of birds and mammals, that a very large part of research upon them from this point of view has been given over to reactive capacities— nest building, social activities, colour change, displacement reactions, etc. but except in so far as they also involve some of the techniques already mentioned, e. g. the use of training methods as indicators of modifiability of behaviour, they do not help materially in this discussion. Some exception should be made here for a few studies of schooling behaviour. These have been summarized by MORROW (25).

II. The Sensory Perception by Fish of Factors of Hydrographical Importance as shown by the Method of the Conditioned Response Experiment.

1. General.

My own personal contribution to this discussion falls under this head. It arose out of and against the background of a primary interest not in fishery problems but in the fundamentals of behaviour. Only after the work was well advanced did I realize its implications for fishery research and modify my programme to take account of this changed emphasis in outlook. But the outlook is still based on the academic study of conditioned reflexes and a few words about it may put it in proper perspective.

Like the date of the invention of soap it seems hard to find precisely who made the first laboratory experiment on conditioned reflexes. The honours are about equally shared among four people. A thesis by WOLFSON (38), Petrograd 1899, in which conditioned salivary reflexes were called psychic reflexes appears to have been the first actual paper.

The second is by Sir CHARLES SHERRINGTON (33) brought to light in this connection by H. S. LIDDELL (23) writing the chapter on conditioned reflexes in FULTON's "Physiology of the Nervous System". SHERRINGTON had been studying the limits of cutaneous anasthesia in a young dog, using for shock purposes an inductorium with a noisy vibrator. Six weeks after spinal transection the animal was being used for the study of vasomotor reflexes, in the course of which closing the key of the same inductorium with the noisy vibrator (though for test purposes only and not connected up to the animal) was found to be followed by a conditioned cardiac inhibition, the heart beat falling from 180 to 54. This was found to be a stable conditioned reflex and clearly the result of the earlier unpleasant skin experiments.

The term 'conditioned reflex' was first used in print by TOLOCHINOV (35) in his report — to a Congress of Natural Sciences at Helsinki — of work completed in 1901. TWITMYER (36) in a thesis called "A Study of the Knee Jerk" reported that during minor adjustments with the subject a bell which had been sounded several times previously and simultaneously with repeated blows on the knee was sounded accidentally without the blow. A kick took place in all respects, both in its kinaesthetic sensations and the objective record, like the true reflex kick. It seems probable that all these four people were noticing these things about the same time and independently of each other.

PAVLOV himself did not publish his own first paper (26) until the year after he had been awarded the Nobel Prize for medicine for his work on digestion on which he had even then been working for 25 years.

KALISCHER (22) and BECHTEREFF (3), both Russians, were very early workers on the subject. It would, however, be wrong to suppose that the fundamental idea behind the conditioned reflex was so recent as this and there is abundant evidence from both philosophers and writers since the time of JOHN LOCKE that the principle of conditioning was familar. Moreover, many of the famous zoologists of the beginning of this century, LLOYD MORGAN, LOEB, THORNDIKE and others, developed forms of animal training techniques whose underlying basis was closely allied to the same general concept. More recently the important contributions to fish perception made by FARKAS (13), VON FRISCH (15), DIJKGRAAF (11), WOHLFAHRT (37), ZUNINI (39) and others working principally with *Phoxinus laevis* have been made by the use of similar association techniques.

There is, however, perhaps a subtle difference between them, but this is not discussed here.

The 'knee jerk' and 'salivation' are typical examples of inborn 'simple' reflexes submissible to physiological analysis, and of which, in some cases, the nervous pathways involved are accurately known. For the development of theory it is useful that this should be so. These are called 'unconditioned' reflexes. Many examples are known in vertebrates, involving both smooth and striated muscle, glands and blood systems. Useful ones in fish are the change in skin resistance leading to a jump in response to electric shock, and eye movements in response to rotation. Complex actions on the same basis, e. g. motor actions to seize food, are more useful in fish. These actions then become known as 'unconditioned responses' leaving their true nature still not precisely defined.

It was established by PAVLOV and his co-workers using salivary reflexes in mammals, and by KALISCHER and BECHTEREFF using motor reflexes, that these inborn actions could be evoked by quite different unrelated previously neutral stimuli, whether through

extero- or intero-receptory systems if certain rigid procedures relating to their juxtaposition in time and circumstance were followed. The process was called 'conditioning' and the new reaction a 'conditioned reflex'.

High technical achievement in respect of experimentation was demanded—the rooms and buildings were sound-proofed, the experimenter isolated from the animal, operations made as silent as possible to exclude extraneous interference. Many terms expressive of the precise way in which the conditioning was carried out were coined—thus we have simultaneous, delayed, trace, etc. conditioned reflexes according to whether the conditioned and unconditioned stimuli are presented together, or with the conditioning one allowed to act for some fixed interval of time before and until the giving of the unconditioned, or at some fixed interval before and then a lapse of time, etc. Discrimination between one closely allied stimulus and another could be achieved by reinforcing the one and not the other.

Examples of all these as conditioned responses may be found in my experiments with fishes. There may also be conditioned reflexes of the first, second, etc. order according to whether they are formed directly on the basis of an unconditioned reaction or secondarily on a previously established conditioned reflex which thus takes on the rôle of the primary reflex. Examples of these also may be found in fishes.

The work of Pavlov and his school, although it had reached large and impressive proportions, remained curiously little known to the scientific world at large until after his Croonian Lecture to the Royal Society in 1923.

With the publication of translations of his books in English in 1927 and 1928, and the appearance of J. B. Watson's "Behaviourism" shortly before that time, conditioning became a common topic. The basic content of "Behaviourism"—as of some other theories of higher nervous activity—was that education, training, all forms of modifiable behaviour, were essentially the foundation of conditioned reflexes of greater or less complexity. This view is still held by many people. It was supposed then, though this is no longer so, that the cerebral cortex was essential for their elaboration.

I had started to take an interest in these problems in 1926, and when, at the Plymouth Laboratory of the Marine Biological Association, Dr. Allen gave me the problem of conditioned reflexes in fishes to see what I could do with it, this question of cortical control of behaviour was prominent in my mind in formulating the programme. These questions are discussed in my first paper, and need not be further considered.

What the Convener and Mr. Graham have specially asked me to do here, on this occasion, is to give you a condensed statement of the methods I have myself used in studying sensory discrimination in fishes, and a summary of the results I have so far obtained.

Except for five years when I was away on war service the work has occupied much of my time over the past 25 years. It will be understood, therefore, that some aspects of it are more sharply focussed in my mind's eye than others.

The experiments may be conveniently divided into two broad classes, depending on whether an electric shock or food has been used as the unconditioned stimulus. These classes in turn fall also into a number of phases.

2. Preliminary Experimentation.

a) Experiments with electric Shock as Unconditioned Stimulus.

Shortly before I started, J. P. Froloff—working in Pavlov's own laboratory—had established conditioned reflexes in fishes using an electric shock as the unconditioned stimulus and the subsequent flight reaction or jerk as the registrable response. He used both light and sound as conditioning stimuli. Conditioned reflexes could be obtained with either of them.

My first venture was to repeat this in a modified form. Not much of the work done by this method will be of direct interest to you, but as I am likely to use it, for a number of reasons, in studying the ability of fishes to detect pressure changes, it may be found helpful to have this account at this stage.

Froloff (16) suspended his fishes with a hook and recorded their movements directly by Marie tambour and lever. I preferred to keep the fish free. Figure 1 shows the general arrangement as used in studying visual conditioning.

The general procedure each day was to take the fish from its normal home in the aquarium and place it in the apparatus about 30 minutes before the first conditioning experiment. The conditioned stimulus was then given at intervals of a few minutes—immediately followed (on each occasion) by the electric shock from a single make-and-break of the coil circuit. To this latter the fish gives a sharp movement. The object was to see whether the fish—after repeated coincident presentations of the light or other stimulus to which it had previously been shown to be indifferent—would make a similar decisive movement to that alone, when given without shock.

Normally, between 5 and 10 such presentations were made daily. After a short period of rest following the last of these the fish was then returned to its place in the aquarium to resume its usual activities until the next day.

Froloff's observations were confirmed. *Blennius gattorugine* and other fishes readily formed such conditioned movements to visual stimuli. (Shown in Table 1 in J. Mar. Biol. Assoc. U.K., N.S., XX(2); p. 367).

When the response is well established, evidence of sensory discrimination is found by introducing a second 'signalling' stimulus at irregular intervals and always without the electric shock associated with the

original conditioning stimulus. The fish now continues to react positively as before to the original stimulus but not—if discrimination is possible—to the second one. (This is shown on p. 361 in J. Mar. Biol. Assoc. U. K., N. S., XX (2) by one example of the daily log of an experiment with *Blennius pholis*).

With this specimen the experiment began on 12th January. It gave the first conditioned motor response to the circle of magenta light (Wratten filter No. 32) on the 6th day and at the 21st trial; the response was stable by the 39th trial; and from the 40th trial onwards to the conclusion on 24th April was given at 126 out of 138 presentations. The 8 trials when no response was given were the first tests made on several different days. Discriminated colours also often produced a positive response at the first presentation in a daily series, though not at succeeding ones. With this general technique it was found possible *inter alia* to make a close study of wave-length discrimination in *Blennius pholis* L. (6). The conclusion was that this fish, whether dark-adapted or not, had a well-developed colour vision as we ordinarily speak of it. Some thousands of trials were made in the course of this study.

No other major work has yet been done by this method. *Anguilla vulgaris* was positively conditioned to an auditory stimulus; but similar work with *Gasterosteus aculeatus*, *Cottus bubalis*, *Pleuronectes platessa*, and *Gobius minutus*, was inconclusive. Not all the fish used could be visually conditioned. Pleuronectid fishes showed no signs of forming the association after 200 trials. Most fishes did so in less than 40. (See Table on p. 362 in J. Mar. Biol. Assoc. U. K., N. S., XX (2)).

It appears from this—and from other evidence from a different kind of conditioning experiment (6)—that the normal reactions of fishes to harmful or threatening influences control the readiness with which conditioned motor reactions are built up, when these are based on such stimuli. This is a good example of the value of field knowledge in interpreting experimental data.

Time will not allow me to give you further details of the experiments under this heading, but it has been seen that the design is a useful one. It can be adapted to many purposes.

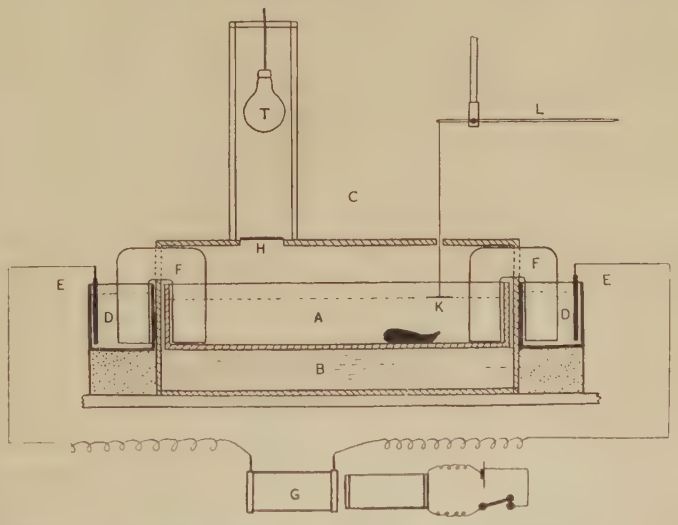
b) Experiments based on Food as Unconditioned Stimulus.

At the same time as I was doing the work just described I was also making other comparatively simple experiments. What I wanted was some simple but unequivocal act of an unconditioned nature which was less harmful and more natural than that resulting from an electric shock. This was found in a food-getting response. For sedentary, crevice-loving fishes (e. g. *Blennius*), this response was to come out of a bottle or other recess to a fixed feeding place. For active, free-swimming, fishes such as *Gadus* it involved swimming into a special food compartment or place, entry into which had to be learned. Whichever is used, the fishes themselves live for the whole duration of the experiment in the special apparatus.

a) **Sedentary fishes.** The habit, which *Blennius* has, of taking up its permanent home in an empty jar or shell or some corner of an aquarium makes it ideal for this work. (It is unfortunate perhaps from my point of view that it is not also our principal food-fish!)

An early piece of apparatus, as used for salinity conditioning, is shown in Fig. 2. This shows the experimental arrangements in simple form.

The fish lives in the jar J. When food is introduced through N the fish comes out to below N, takes the



A, Fish (*Blennius*) in shallow glass trough; B, sound-absorbent packing; C, screening box; D, E, F, non-polarisable electrode system—D, glass jars with saturated solution of zinc sulphate, E, zinc plates leading to terminals of Harvard induction coil, F, agar-agar-seawater bridges leading current into fish trough; H, T, the visual stimulus system; K, L, recording device—K is a microscopic coverglass greased with vaseline on both sides, giving a high surface tension. This floats on the surface of the water. It is attached with waxed thread to the short arm of a sensitive lever, adjusted to maintain a tension on the thread and to be itself horizontal when at rest. The slightest water movement gives a large deflection in the long arm. An aeration system was present but is not shown.

Figure 1. Apparatus used in studying visual conditioned responses in fishes when an electric shock is the unconditioned stimulus. From J. Mar. Biol. Assoc. U. K., N. S. XV (2), p. 525, fig. 16.

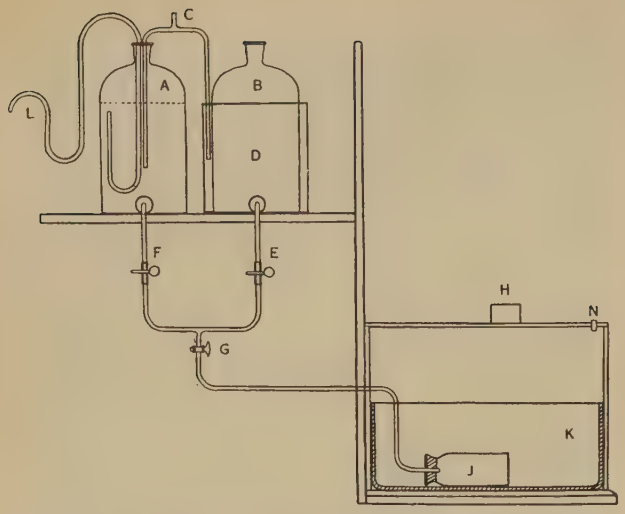


Figure 2. General view of early apparatus used with *Blennius* for the study of conditioned motor responses to salinity changes. From J. Mar. Biol. Assoc. U. K., N. S. XV (2), p. 503, fig. 5.

A–G, salinity change system: A, B, aspirators; C, to sea-water supply; D, outer jacket to B, supplied through C; E, F, exits from aspirators A, B, meeting at G; L, constant-level tube: Aquarium K houses fish in bottle J; H, periscope for observation from outside screen; N, feeding tube. Right-half of diagram separated from left-half, and also screened from the front.

food, and returns quickly to its pot. This is the unconditioned motor response. The normal flow of water over the fish in J was through AFG, into K and then to waste; by closing F and opening E water of any desired salinity could be substituted. Having, at that time, no idea of how the experiment would proceed, I made the first changes drastic, using fresh water for the stimulus. Repeated trials with this before conditioning was started showed that it was characteristic of the fish to retreat as far as it could go to the back of the pot, rather than to come out. It was desired to see if repeated presentations of this change-over from sea water to fresh water for 15 seconds with the giving of food at N after a constant time interval of a further 15 seconds would result in the production of the motor response involved in food-getting.

Thirty such presentations, spread over the period 8 April—8 May, produced no signs of activity or 'appreciation' in the fish. In the course of the next three days the conditioned response showed up gradually. It showed first as a tentative head-movement, then as part-body movement, and finally as complete movement to the food-tube. In the fully-formed and well-established response, 'psychological' anticipatory characteristics, such as mouth-champing, pectoral-waving, and eye movements were also noted. The magnitude of the change was then made successively less at succeeding trials: The fish still made the fully formed response. Whilst the response was still being given to a change of 3 $^{0}/_{00}$ the experiment was concluded. At this time however the work was still largely exploratory. I deal later with salinity discrimination in more detail.

A number of other experiments with *Blennius* fall into the same exploratory category with this type of arrangement. Thus, several specimens were shown to be able to form this particular motor conditioned response to temperature increases, to changes in direction of current-flow, and to gustatory, but not to olfactory, stimuli.

Temperature discrimination is dealt with later.

A change of 90° in direction of current-flow served as an effective conditioning stimulus in each of seven individuals. When conditioned to this change all seven showed the conditioned response to changes greater than this (up to 157.5°). Five out of the seven gave no evidence of discriminating changes of less than 90°; in the other two there was some, but only slight, evidence that they did so.

Gustatory stimuli which would serve as effective conditioning agents included extracts of Nereid worms, *Mytilus*, and *Patella*, all prepared by grinding with sand and vacuum filtration. Amounts of 0.01 $^{0}/_{0}$ in sea water, introduced into the stream flowing past the fish, were found—after generalisation from a stimulus much stronger than this—to be perceived. A remarkable feature of the gustatory experiments was that some of the fishes would turn round and bite at the incoming solution before carrying out the correct response.

True olfactory stimuli which, at the same time, have no other effect on sea water are hard to find. Those used, but giving wholly negative results, included artificial musk (Trinitro-butyl-toluene)—a perfume of cheap soaps—and the water obtained by merely leaving Nereid worms in contact with a standard amount of sea water for some hours.

β) **Free-swimming fishes.** The early work under this head, although crude, was most effective.

As I said before, the response here involved swimming into a special food compartment. Food was introduced into this chamber by washing it down with water through a tube. Some preliminary training of a not very subtle kind was needed to bring fish to realise that the food chamber was, in fact, the place where food was to be found.

The general pattern is shown in Figure 3; its adaptation for studying auditory discrimination in *Crenilabrus* in Figure 4.

An example of the technique may be given. Routine procedure at each test, repeated several times a day, was as follows:— the tuning fork is started; 15 seconds later a piece of Nereid worm is sent into the bottle (which is translucent); the fish swims into the bottle and fetches food; the sound is then stopped. No reaction of any kind is seen at first to the sound alone. One fish went straight to the bottle and waited for food after only 20 such coincident presentations. After this was well established an additional food chamber

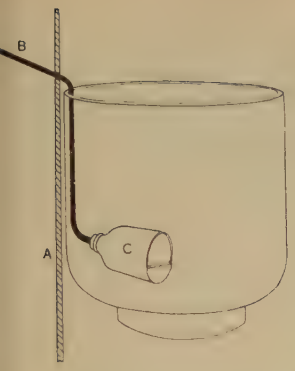


Figure 3. Arrangement of food-chamber in preliminary experiments on conditioned responses in free-swimming fishes. From J. Mar. Biol. Assoc. U. K., N. S. XV (2), p. 512, fig. 10.

A, partition separating apparatus from observer; B, tube through which food is given; C, food-chamber (glass reagent bottle from which bottom has been removed, leaving a small lip).

was placed at the other end of the tank; this was used with the sound of an electric buzzer immersed also at that end. The fish readily learnt to associate the right sound with the appropriate food chamber; but it was later shown that this was based on their positions and not on its ability to distinguish one sound from the other.

With this general arrangement conditioned visual responses were also established in several Labrid fishes, in *Pleuronectes platessa*, *Gadus virens* and *Gadus callarias*. The Labrid fishes showed ability to distinguish between one light and two, and gave some, but not convincing, evidence of colour discrimination. It is emphasized here, however, that these experiments were, at that time, still largely exploratory; that they should not be taken too seriously from this secondary aspect. Their principal aim was to find out the validity of the method and its possibilities.

3. Provision of Special Building.

By 1932 I had gathered together a great deal of information on my primary object—the general characteristics of conditioned response formation in fishes. I also felt that the validity of the method in studying sensory discrimination was established, but I had had to work in ordinary laboratory conditions (or much worse!) with their attendant difficulties for this kind of problem. I had done what I could to lessen vibrations and reduce the effect of other extraneous stimuli, but thought that more should be done. Pavlov stressed the need for care over this; von Frisch and others appeared to prefer the general buzz of activity in a busy laboratory. My own experiences supported Pavlov. In 1932 therefore a small, but inexpensive sound-insulated building was built at the Cullercoats laboratory. This met some of the requirements and removed many causes of anxiety. At any rate, it was no longer a miserable hole or corner to which one hardly dared to invite a colleague. Visitors to a Challenger Society Meeting at Plymouth in 1927, who saw one of my early experiments on visual conditioning in *Labrus berggylta* may perhaps remember the 'black hole of Calcutta' (as my wife called it) in which it was done!

4. Definitive Experiments on Sensory Perception using Technique b.

This special building enabled me to concentrate on factors which are important from the fisheries' standpoint. Emphasis was shifted from academic problems to such purely technical ones as keeping fishes (especially the major food fishes) alive and healthy in confined spaces for long periods, and of isolating the particular stimulus being investigated. None of these was complicated in the sense that a radar set is complicated, but to ensure the purity of the stimuli was not easy.

All the experiments now to be discussed fall into the class of conditioned responses just described, i. e. the unconditioned response is food, and the conditioned response which it is sought to establish is that of swimming into a special food compartment. The successful formation of the response is taken as evidence that the fish objectively perceives the stimulus upon which it has been built. After the conditioned response is firmly established the magnitude of the conditioning stimulus is gradually reduced at successive trials. The strength next above that at which it fails to elicit the response, after repeated trials, is taken as the lower limit of perception.

In the experiments of this class which I have already mentioned, the fish was free to swim where it pleased. No restriction whatever was placed upon its movements. The result was that some of the specimens—even of the actively swimming species—came to take up a more or less permanent position in the food compartment! Neither could I use that kind of tank for work involving changes in the physical or chemical properties of the water. It became essential then to have a system with a number of desirable properties. It should be

(i) still practicable for the fish to perform some clear-cut motor response,

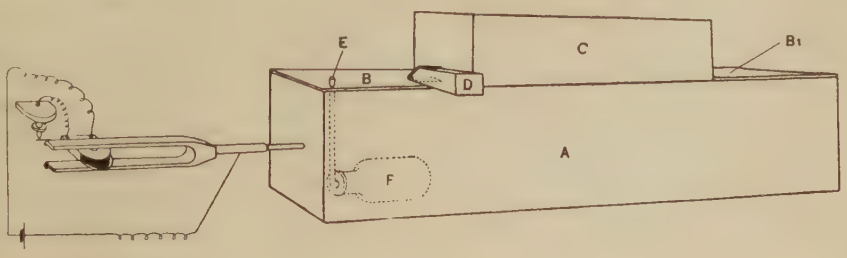


Figure 4. Apparatus used in the formation of conditioned responses in *Crenilabrus melops* towards auditory stimuli. From J. Mar. Biol. Assoc. U. K., N.S. XV (2), p. 508, fig. 8.

A, tank housing fish; B, C, screening arrangements; D, periscope for observation; E, tube leading to food-chamber, F.

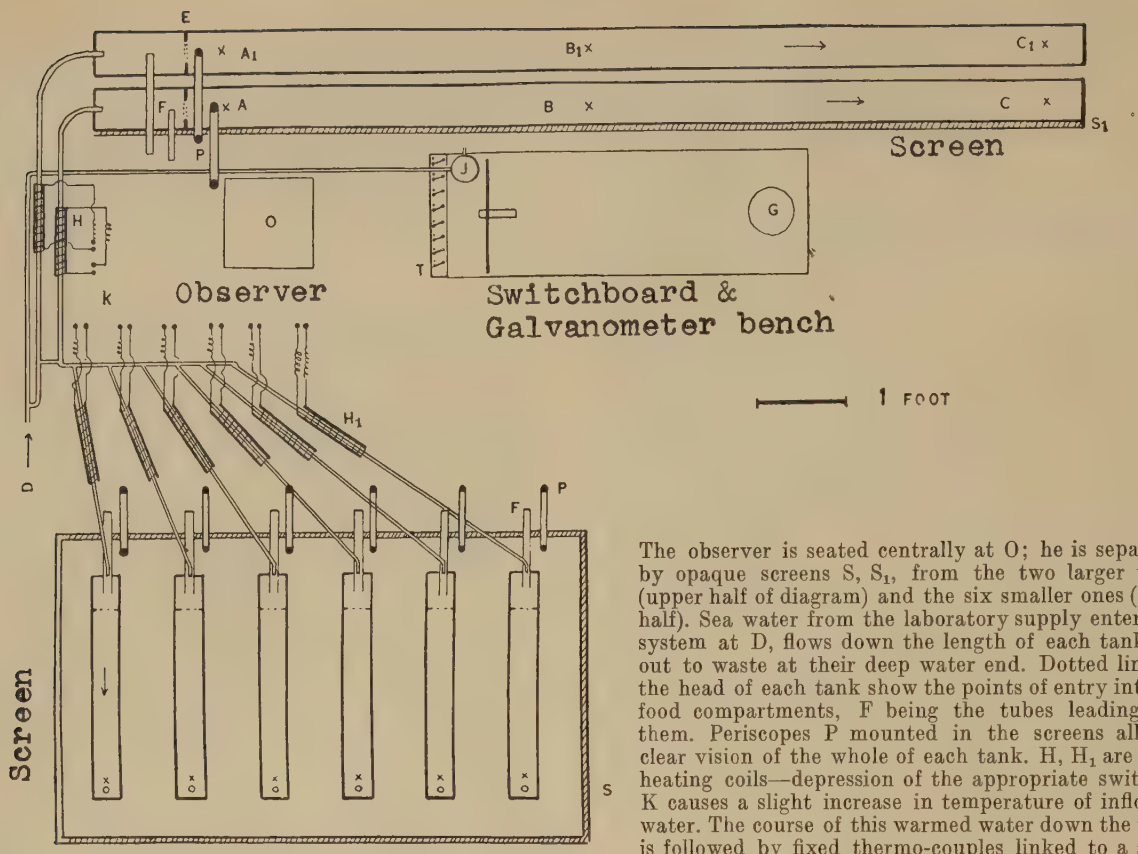


Figure 5. Plan of lay-out used in formation of conditioned motor responses in fishes to slight temperature rises. From J. Mar. Biol. Assoc. U. K., N. S. XXI (1), p. 5, fig. 2.

The observer is seated centrally at O; he is separated by opaque screens S, S_1, from the two larger tanks (upper half of diagram) and the six smaller ones (lower half). Sea water from the laboratory supply enters the system at D, flows down the length of each tank and out to waste at their deep water end. Dotted lines at the head of each tank show the points of entry into the food compartments, F being the tubes leading into them. Periscopes P mounted in the screens allow a clear vision of the whole of each tank. H, H_1 are small heating coils—depression of the appropriate switch at K causes a slight increase in temperature of inflowing water. The course of this warmed water down the tanks is followed by fixed thermo-couples linked to a sensitive galvanometer. The observer is able to make all manipulations without movement of his body and without noise.

(ii) impracticable for the fish to stall the experiment by 'squatting',
(iii) adaptable for making changes in the properties of the water with precision,
(iv) practicable to measure or record such changes,
(v) possible for all these things to be done without giving extraneous cues.

Not all these objectives were achieved at once. Most of them could, I thought, be achieved by using long, narrow, inclined tanks. The inclination could be such that there was a shelving depth of water—from little or none at one end to a comfortable and sufficient depth at the other. The food compartment was to be at the head of the tank. Under the compulsive stress of hunger—and by gradually introducing food further and further upstream at successive feedings—it was thought that the fish could be brought to make this rather hazardous movement along the whole length of the tank into the food compartment. It would certainly return if it could.

The first two years in the new building were spent mainly on temperature perception in marine teleosts using these arrangements.

a) Temperature Perception.

The experiments on temperature perception were lengthy; some taking many weeks or even months; numbers of them were therefore carried on simultaneously. Figure 5 shows how this was done.

The following extract from a published paper (8) describes procedure. It is quoted almost in full as illustrating generally the day-to-day details of most of the work I have still to bring before you.

"The observer enters the building and locks both doors. The tanks are inspected to see that the water flow, etc. is all in order. He then takes up his position ... on the stool 0 and notes the behaviour and position etc. of the fishes during at least fifteen minutes, the temperature of the cold water junction is read, and the galvanometer readings for each thermocouple are taken. Then the following operations are carried out for each tank. The switch of the heating circuit is closed ... Records of the galvanometer readings are ... noted down ... food is introduced into the ... food chamber ... one piece at each association. To the first of the two stimuli—the temperature increase—the fish shows no signs of response

for a large number of tests. To the second—the food lying in the food chamber—it shows no sign of response until it is perceived (by sight, smell, etc. according to the habit of the fish). A fish such as the cod, for instance, does not react to it for several minutes (i. e. until perceived either by smell or taste or, less likely, by sight) owing to the distance of the food, but when it is perceived the fish at once starts upstream 'seeking' movements, and so persists directly upstream until it gets half way up the tank where it begins to get uncovered. In the early stages of conditioning it now returns to its normal position, and shortly after again goes through the same performance, repeating it several times. Its actions become progressively more excited, at each attempt going further upstream nearer to the food, and in so doing becoming more uncovered with water. Finally it makes a rapid splashing swim ... right into the food chamber, where it makes an attempt to seize the food, acting throughout as if in a state of great agitation. In these early stages it is usual for this to result in failure to acquire the food, whereupon the fish splashes back at great speed to its resting position without the food for which it has struggled. For several days it is not usual for the fish to go through these actions in their entirety more than once in one day, although the food is still present in the food compartment and the fish is free to fetch it. If this remains uneaten by the end of the day I remove it ... As these associations are continued day after day the fish becomes more persistent in its efforts to reach the food and less agitated by its own vigorous splashing. Eventually, when thoroughly conditioned, it takes the food without hesitation, but always, or so it appears, with great excitement, and to the end of the experiments makes the return journey with very great rapidity and nervousness. By continuing this regular association ... there comes a time when ... the fish shows an obviously anticipatory reaction. With fishes such as the gadoids, which maintain posture by gentle undulation of the pectoral fins, the earliest sign of conditioned response is a quickening of their undulation, followed by a rapid swim upstream, of varying extent; and in its final form the whole response occurs in the way already described as the act of food-getting. It must be remembered that this now takes place before the introduction of food. In the later stages the fish, having arrived at the food chamber, continues to wait there practically 'high and dry' until food is given, which it then seizes sharply and swims and splashes back to its normal position.

During these performances the attitude of the fish may be described as one of great excitement and its movements are rapid, alert, and vigorous; it may also show champing movement of the jaws. With sedentary fishes such as *Blennius*, *Onos*, *Liparis*, etc. which remain (under the conditions of these experiments) for hours or even days motionless in their tanks, the response is still more striking."

The effect of the shelving water is to confine the fish, as I have said, to the deeper water at the remote end of the tank. Beyond this, no restriction whatever is placed upon its movements. The precise measurement of the temperature at the moment of stimulation was therefore not easy. As to how this was done reference must be made to the original account (8). It must suffice here to say that my galvanometer gave a spot deflection of 6mm. per 0.1° C. and to stress that I was concerned to measure only the actual rise at the moment of stimulation. The properties of the system, as well as of water itself, made it inevitable that the fish remained under the influence of the 'warmed' water long after this moment, and for the most part also long after food had been taken and the reaction of the fish had subsided. But this circumstance has no relevance.

Bearing in mind that the course of the experiments was to start with a considerable rise (of anything between 0.4° C. and 3° C.) in temperature as the conditioning stimulus; and that, after conditioning was established, the magnitude of this was then successively reduced; I may now summarize the final results. (See Table 1, from Table 3, p. 24, J. Mar. Biol. Assoc., U. K., N. S., XXI (1).)

b) Salinity Perception.

When the experiments on temperature discrimination were finished I took up the study of the ability of fishes to perceive changes in salinity and later of pH.

In order to do this it became necessary to follow in detail what happens when water flows down the kind of tanks I was using. Introduction of indicator solutions showed that the actual course of the water layers was—at any rate to me—quite unexpectedly complex; it might not, I suppose, have proved so to a student of hydraulics. I could certainly not use the tanks as they were for chemical changes of any precision. It was found, however, that if the inclination of the tanks is reversed—so that the gradient is uphill, with the water entering at the lower end and flowing to waste over a rim at the upper end—then the path of introduced solutes is (almost equally surprisingly) simplified. Instead of tracing out complicated swirls it moves steadily forwards—supplanting the original water—forming a practically straight front as it moves along the length of the tank. This was the first change made. The tanks were also further modified by the addition af a small limb, making them into L-shaped troughs (see Figure 6, 1—5).

This L-shaped tank is to me what the maze was to Small, the inclined plane to Crozier, the problem-box to Thorndike!

Such a tank with a slope of about 1 in 30 has a few cm. of water at the lower or deeper end shelving to none at the upper. Fishes placed in it come to take up a more or less permanent position in the short limb—either slowly swimming about in it (e. g. *Gadus*) —or stationary, curled up in one of the corners (e. g. *Blennius*).

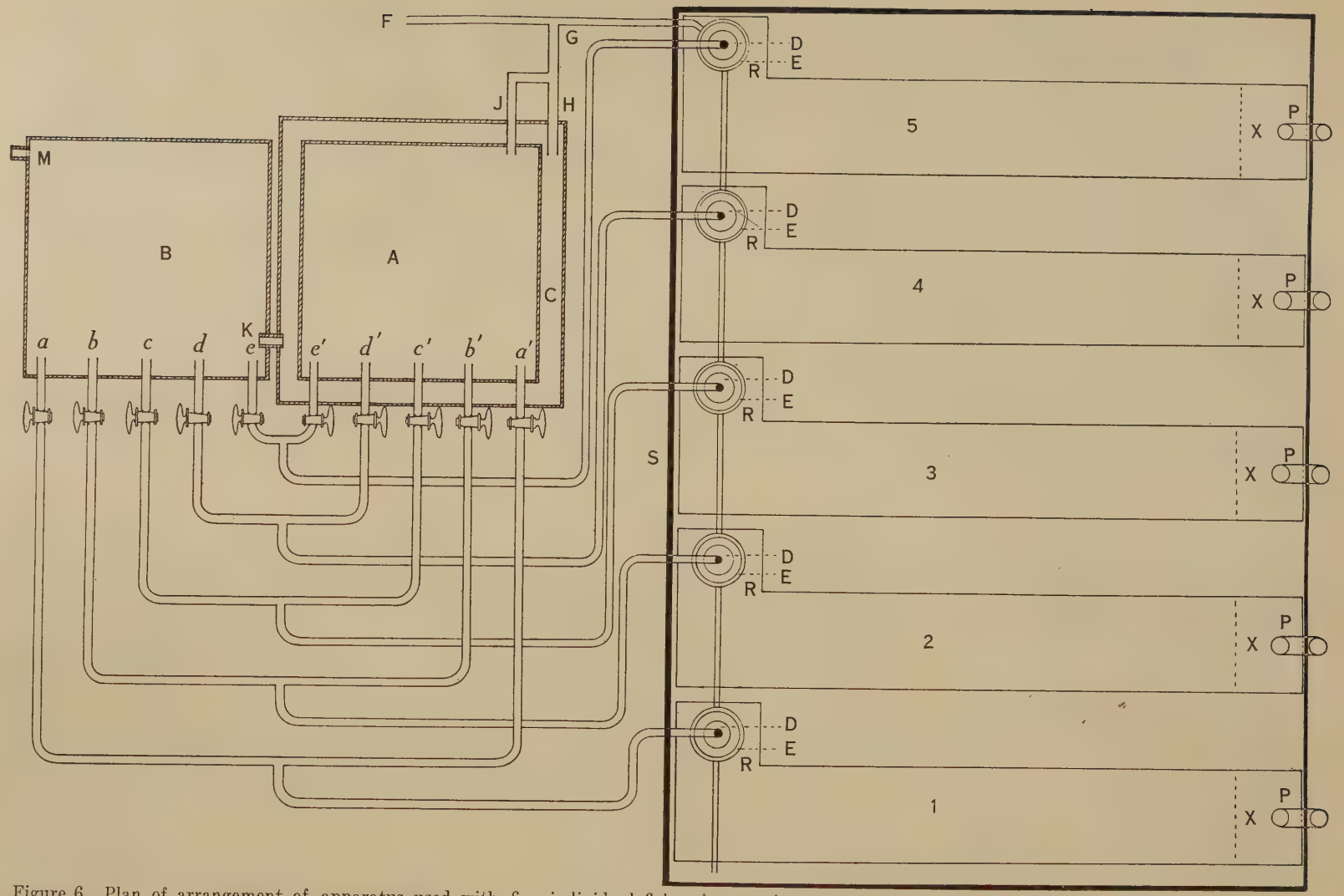


Figure 6. Plan of arrangement of apparatus used with five individual fishes in experiments on salinity discrimination. Note: Right-hand side of assemblage reduced 1.6 times more than left-hand side. From Rep. Dove Mar. Lab. 3rd ser., **5**, p. 24, fig. 1.

Legends to Figs. 6 and 7. A, reservoir for stimulus water: B, normal sea water supply. also circulates through C, outer jacket to A; flow goes from a—e (or a_1—e_1) through screen S, to tanks 1—5 in that order: Before entering individual tanks the flow is broken by the constant-level device D, (the head of which is lower than the bottom of the reservoir)—thus making rate of entry into tanks constant and independent of slight changes in A, or B; E, Davies's double-surface condensers; sea water supply to whole system from F, through G simultaneously to reservoirs and condensers; tanks 1—5 slope upwards 1 in 30 from R to P; fishes live below E at R; food-chambers at X; P, periscopes for individual observation; T, overflow.

Summary of experiments on formation of conditioned responses in fishes to a rise in temperature.

Table 1.

Species	Number of associations required for production of conditioned response to thermal increase	Total number of associations in experiment	Minimum effective thermal conditioned stimulus °C.
Spinachia vulgaris FLEM.	41	84	0·05
Nerophis lumbriciformis (PENNANT)	56	76	0·07
***Gadus callarias* L.**	18	61	0·05
***Gadus merlangus* L.**	10	73	0·03
***Gadus virens* L.**	24	83	0·06
Onos mustela (L.)	12	29	0·03
Raniceps raninus (L.)	31	147	0·05
Blennius pholis L.	33	95	0·03
Chirolophis galerita (L.)	25	33	—
Centronotus gunnellus (L.)	39	95	0·03
Zoarces viviparus (L.)	25	95	0·03
Gobius flavescens FAB.	14	77	0·05
***Pleuronectes flesus* L.**	20	59	0·05
***Pleuronectes platessa* L.**	11	71	0·06
	21	78	0·05
Cottus scorpius L.	12	88	0·05
Cottus bubalis EUPHRASÉN	27	108	0·03
Cyclopterus lumpus L.	32	67	0·05
Liparis montagui (DON.)	26	71	0·03
Crenilabrus melops (L.)	29	71	0·05

From J. Mar. Biol. Assoc. U.K. NS. XXI (1), p. 24.

Five of these (shown in thick type) are fishes of importance commercially.

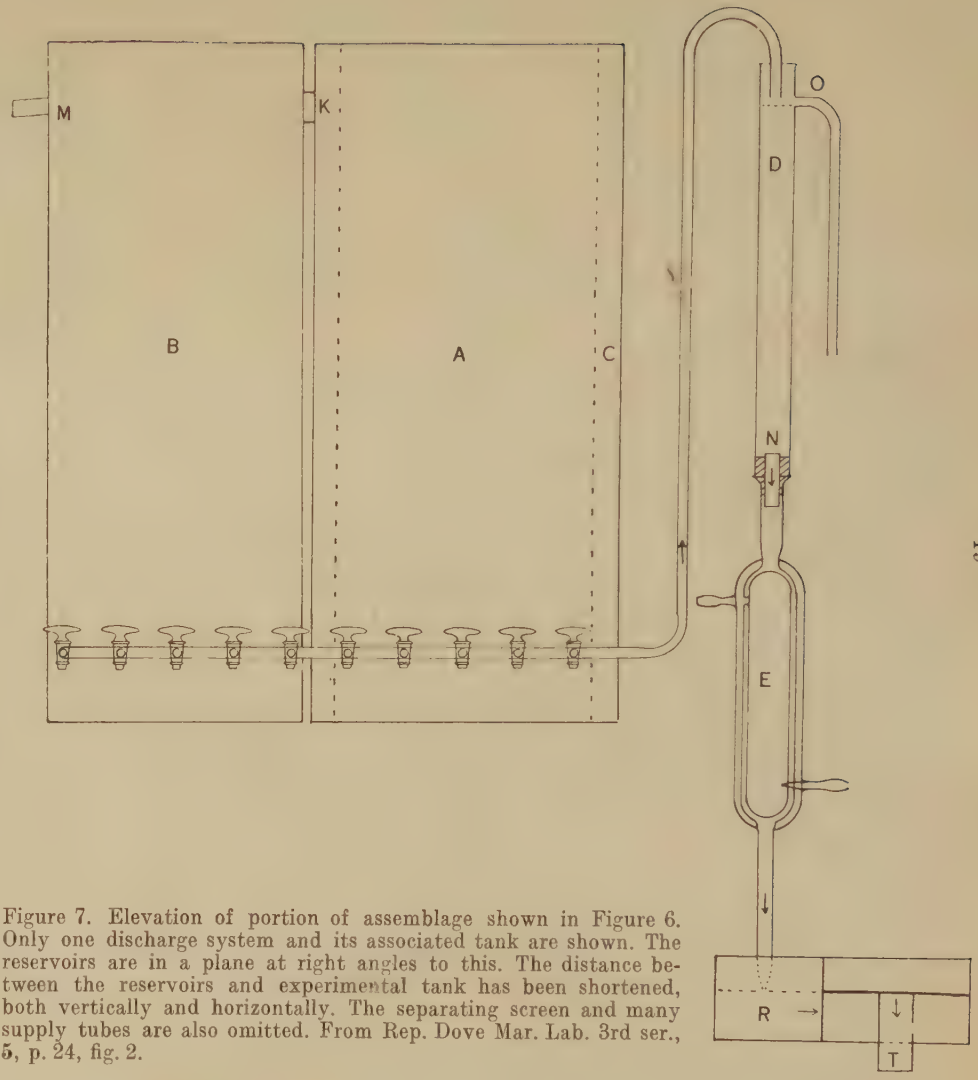


Figure 7. Elevation of portion of assemblage shown in Figure 6. Only one discharge system and its associated tank are shown. The reservoirs are in a plane at right angles to this. The distance between the reservoirs and experimental tank has been shortened, both vertically and horizontally. The separating screen and many supply tubes are also omitted. From Rep. Dove Mar. Lab. 3rd ser., **5**, p. 24, fig. 2.

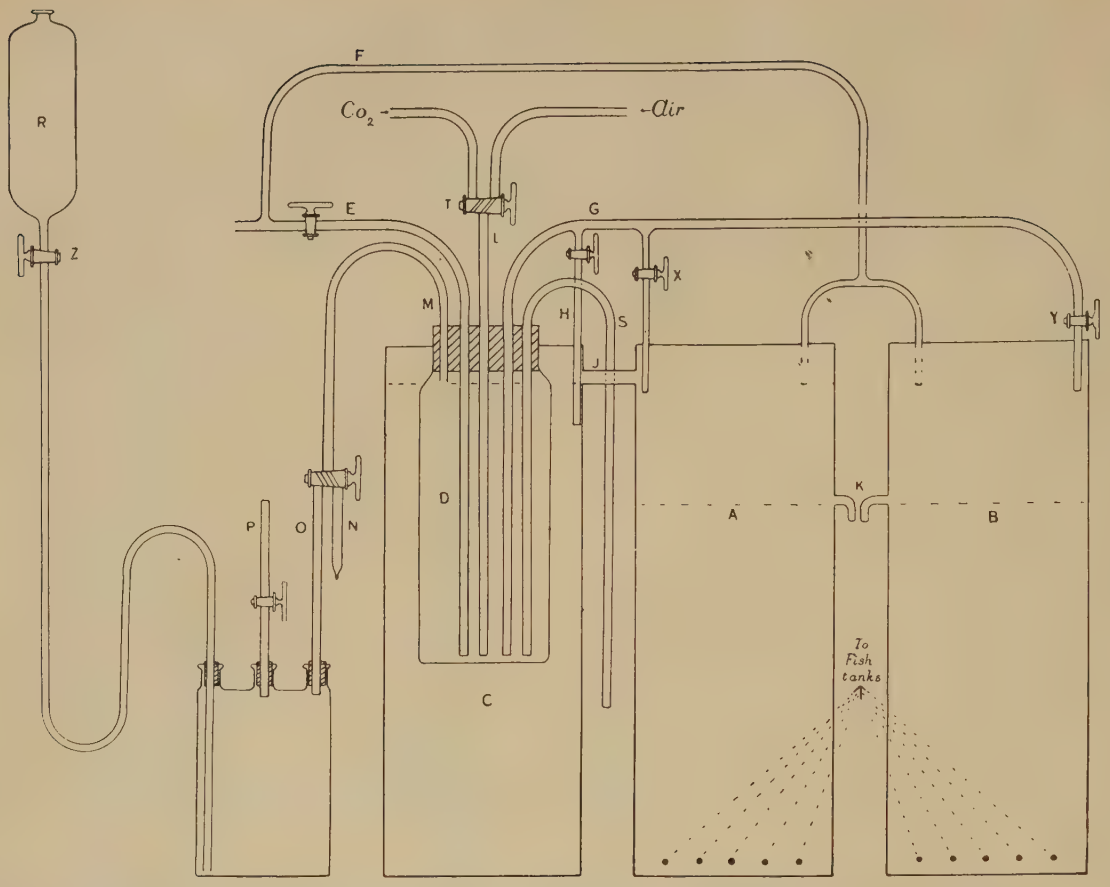


Figure 8. Diagram of apparatus used in production of pH changes as conditioning stimuli in fishes. The ten outlets on the right lead to ten tanks arranged as shown in Figure 5. From Rep. Dove Mar. Lab. 3rd ser., 7, p. 23.

A, B, supply reservoirs to fish tanks—after leaving reservoirs the arrangements are as in Figs. 6 and 7; changes could be made separately in either A or B; sea water supply from F has off-shoot at E for preparation of stimulus-water in 'acid-reservoir' D; water flows through D up to time of preparation, then via C and G; L, two-way cock to CO_2 supply or compressed air as required; M, the same leading to atmosphere or Wolff's bottle system as required; N, tap for withdrawal of samples for pH; CO_2-saturated water equivalent in amount to that placed in funnel R could be discharged into A or B by the Wolff's bottle system and manipulation of the appropriate stopcocks.

Table 2.

Species	Specimen	A	B	C
***Pleuronectes platessa* L.**	1.	18	82	0·17
***Pleuronectes platessa* L.**	2.	33	67	0·23
***Pleuronectes platessa* L.**	3.	98	190	0·17
***Pleuronectes flesus* (L.)**	1.	20	78	0·17
***Pleuronectes flesus* (L.)**	2.	9	52	0·23
***Pleuronectes flesus* (L.)**	3.	87	190	0·17
***Gadus merlangus* L.**	1.	30	177	0·17
***Gadus merlangus* L.**	2.	39	190	0·17
***Gadus virens* (L.)**	1.	37	176	0·17
***Gadus virens* (L.)**	2.	28	190	0·17
***Gadus callarias* L.**	1.	26	177	0.23
***Gadus callarias* L.**	2.	29	190	0·17
Onos mustelus (L.)	1.	20	87	0·23
Onos mustelus (L.)	2.	6	67	0·17
Centronotus gunnellus (L.)	1.	23	80	0·17
Centronotus gunnellus (L.)	2.	—[1])	87[1])	—[1])
Centronotus gunnellus (L.)	3.	15	67	0·45
Blennius pholis L.		17	82	0·45
Zoarces viviparus (L.)		22	76	0·23
Liparis montagui (Don.)		46	79	0·45
Gobius flavescens Fab.	1.	11	75	0·06 (0·11)
Gobius flavescens Fab.	2.	27	67	0·06
Cottus bubalis Euphrasén	1.	29	76	0·23
Cottus bubalis Euphrasén	2.	18	67	0·45
Cottus scorpius L.		27	54	0·17
Nerophis lumbriciformis (Pennant)		76	176	0·45
Crenilabrus melops (L.)		63	177	0·45
Gasterosteus aculeatus L.		26	74	0·23
Spinachia vulgaris Flem.	1.	27	48[2])	0·56
Spinachia vulgaris Flem.	2.	14	51	0·23

A Number of associations required for production of conditioned response to salinity stimulus

B Total number of associations between food and salinity stimulus in completed experiments

C Minimum effective salinity change required to produce conditioned response when well established. Parts per thousand

[1]) Not conditioned. [2]) Prematurely finished.

The species in thick type are fishes of importance commercially.

From Rep. Dove Mar. Lab. 3rd ser. 5; p. 32.

Table 3. Summary of numerical features of conditioned response formations in Teleostean fishes towards a reduction in the pH of the sea water flowing past them.

Species	Specimen	Size of Fish. cm.	Number of associations required for production of first conditioned response to change in pH from 8.0 to 7.0 (approx.)	Total number of associations between food and change in pH in whole experiment.	Minimum pH difference perceived.
Anguilla anguilla (L.)		15·7	84	160	0·05
Nerophis lumbriciformis PENNANT	1.	11·6	51	210	0·05—0·07
Nerophis lumbriciformis PENNANT	2.	12·4	53	173	0·05
Gadus callarias L.	1.	9·5	20	181	0·04—0·05
Gadus callarias L.	2.	13·0	44	181	0·04—0·05
Gadus merlangus L.	1.	12·6	27	181	0·04—0·05
Gadus merlangus L.	2.	12·4	24	181	0·05—0·06
Gadus merlangus L.	3.	9·5	37	160	0·05—0·07
Gadus merlangus L.	4.	8·5	26	160	0·05—0·07
Gadus virens (L.)	1.	9·2	15	181	0·04—0·05
Gadus virens (L.)	2.	9·0	19	181	0·04—0·05
Onos mustela (L.)	1.	13·0	11	173	0·05
Onus mustela (L.)	2.	7·6	10	181	0.05—0·06
Crenilabrus melops (L.)	1.	6·5	27	173	0·05
Crenilabrus melops (L.)	2.	5.3	33	181	0·05—0·06
Gobius flavescens FAB.	1.	5·5	22	210	0·05
Gobius flavescens FAB.	2.	6·0	36	210	0·05
Blennius pholis (L.)	1.	10·2	15	210	0·05
Blennius pholis (L.)	2.	9·8	16	181	0·05—0·06
Chirolophis ascanii WALB.		14·0	17	210	0·05
Centronotus gunnellus (L.)	1.	13.5	18	181	0·05—0·06
Centronotus gunnellus (L.)	2.	15·8	65	160	0·05
Zoarces viviparus (L.)	1.	13·0	45	210	0·05
Zoarces viviparus (L.)	2.	14·0	48	160	0·05—0·07
Cottus scorpius L.	1.	9·5	38	210	0·05—0·07
Cottus scorpius L.	2.	12·5	19	173	0·05
Cottus bubalis EUPHRASÉN	1.	9·0	20	210	0·05—0·07
Cottus bubalis EUPHRASÉN	2.	10·3	17	160	0·05
Gasterosteus aculeatus (L.)	1.	7·5	24	210	0·05—0·07
Gasterosteus aculeatus (L.)	2.	8·5	12	160	0·05—0·07
Spinachia vulgaris FLEMING	1.	9·5	13	210	0·05—0·07
Spinachia vulgaris FLEMING	2.	10·2	30	160	0·05
Rhombus maximus (L.)		8·4	39	173	0·05
Pleuronectes limanda (L.)	1.	10·3	37	173	0·05
Pleuronectes limanda (L.)	2.	12·6	39	173	0·05
Pleuronectes platessa L.	1.	7·2	50	173	0·05
Pleuronectes platessa L.	2.	11·0	76	160	0·05—0·07
Pleuronectes flesus (L.)	1.	7·5	33	173	0·05
Pleuronectes flesus (L.)	2.	9·0	36	173	0·05
Pleuronectes flesus (L.)	3.	9·0	54	160	0·05

From Rep. Dove Mar. Lab. 3rd ser., 7; p. 29.

Figures 6 and 7 show the lay-out of experiments on salinity perception in which five of these tanks were being used simultaneously. The general features of the experiments remained as before. It should be noted, however, that the response, alike in all other respects to that described under temperature perception, is here a downstream one.

The initial stimulus in all cases was a change of approx. 4 ‰, i. e. from 34 ‰ to 30 ‰. Notes were made for each presentation as follows:— Date; serial No; particulars of normal flow, i. e. Cl, T°C, pH, occasionally density and alkali reserve; the same for the stimulus water; condition, behaviour, etc. of fish prior to experiment; time of salinity change-over; response of fish to new salinity—prior to giving food; time food given; reactions to food; time when normal flow resumed.

After conditioning none failed to show a response to a change of 0.5 ‰. One at least of each species gave conditioned responses to changes of approx. 0.2 ‰, i. e. they perceived and reacted to sea water diluted to the extent of 1 ml. fresh water in 150 mls. sea water—but not to the extent of 1 ml. in 200 mls. Titration showed that their limits of perception, in such cases, lay between 0.17 ‰ and 0.23 ‰ using sea water of approx. 34 ‰. *Gobius flavescens* (= *ruthensparri*) perceived differences of 0.06 ‰. (See Table 2, from Table 1, p. 32, Rep. Dove Mar. Lab. 3rd ser., 5).

c) pH Perception.

By this time, I had a standard procedure for the conditioning experiments themselves, which I have described, and with which I need not deal further. My main problem here was to ensure the isolation

and purity of the stimulus. I must stress the need for this purpose of being able to produce the desired change in pH sharply and decisively, several times a day, without fuss or noise, change of temperature, taste, smell, rate of flow, etc. The chemist will at once realise how many apparently trivial difficulties must be overcome to do this. The only practicable way was found to be to add to the normal flow of water known small amounts of a freshly prepared CO_2-saturated sea water of pH 5.0—5.2. For the details, reference must be made to the original paper. Figure 8 shows the system diagrammatically.

The general arrangements were otherwise similar to those of the salinity experiments, except that 10 (in place of 5) separate experiments were carried on simultaneously.

When deciding what methods to use for measuring the pH changes, complete interdependability over a limited range was regarded as more important than absolute figures. For many reasons, therefore, I fell back on colorimetric measurement based on McClendon's borax-boric acid mixtures. Accuracies of ± 0.01 were obtained.

The initial conditioning stimulus for all the fish was a change from the normal sea water (7.95—8.22 pH) to approx. pH 7.0. This was brought about by adding 500 mls. of the CO_2-saturated water to the 10 litres of water maintained in the reservoir and kept continually well-agitated. This change proved to be an effective stimulus, after conditioning. By the generalisation procedure the magnitude of the change required for conditioning was gradually reduced until the point was reached when, after continued trials, no further conditioned reaction could be provoked. Decisive conclusions were reached with 40 specimens covering 20 species, of which 7 are of economic interest. (See Table 3, from Table 1, p. 29, Rep. Dove Mar. Lab. 3rd. ser., 7).

Positive conditioned responses were found to all changes of pH 0.1 or more; and to more than 90 % of those where it was between 0.04 and 0.06. Consistent reaction was not found to less than this. These are the differences between the pH of the normal water and the stimulus water before it leaves the reservoir. There is thus a possibility that the detected change may be less than this.

d) Work Inconclusive or in Progress.

α) **Discrimination of rates of water-flow.** Changes in flow from a linear rate of between 5 and 20 cm. per min. to between 20 and 40 cm. per minute were found not to act as conditioning stimuli in all the fishes listed in the table referred to above. Neither did such changes provoke any other kind of reaction.

The apparatus used was similar to that shown in the right-hand side of Figure 6, but excluding the condenser and individual constant-level systems. The reservoirs were suspended from pulleys. Reproducible variations in water speed were obtained by varying the height of the water level relative to the experimental tank; the rate of flow being calibrated against a scale.

β) **Discrimination of pressure changes.** Experiments are in progress.

III. Conclusions.

Earlier (in section I 2) I posed two groups of questions which I thought might reasonably be put to the student of fish behaviour by this assembly. These were:—

1. Are any features of their normal environment perceived by fish in such a manner as to enable them to make use of them, either voluntarily and intentionally, or involuntarily? If so, are any of them important hydrographically?

2. Are the apparently hereditary behaviour traits of fishes—especially their feeding, shoaling, migratory movements—determined by measurable properties of the seas and rivers? If so, what are they, and are such hereditary traits modifiable by changes in these properties?

In framing these questions I was not thinking of those features—perceived by fish through the familiar senses of sight, touch, etc. and which common observation has shown us to be variously significant for them (though there is still much also to be discovered here)—but of those features for which direct evidence of perception is impossible. I had also principally in mind the most important food fishes.

To all of them the answers are incomplete or fragmentary:

Question 1. The work I have just described permits, I believe, the following contributions to partial but definite answers.

1. Individual teleosts perceive, and react purposively to—as shown by their ability to form conditioned responses—these minimal changes in the water immediately surrounding them:—

(a) 0.03° C. of temperature
(b) 0.2 ‰ of salinity
(c) 0.05 pH

2. Whether they are capable of similarly perceiving changes in rates of current flow has not yet been resolved. So far, the evidence is that they do not perceive such changes when the rates are very slow. There are, however, great practical difficulties in

carrying out the work using rates of flow etc. corresponding to normal tidal flows or oceanographic currents. Large and costly installations would be required.

3. The experiments (like other conditioned response experiments)—whether yielding positive conclusions or not—permit no statement on their "psychological" meaning. But the way in which the responses are carried out suggests that they are different in character to typically involuntary acts, such as the maintenance of equilibrium. In nature, reactions based on these perceptual abilities would probably be both voluntary and intentional.

4. The physical distribution of these properties of sea water is such that they might well serve, on the basis of this evidence, as directive stimuli.

They are therefore important hydrographically; the more so since the perceptual ability of the fish lies close to the limits of accuracy of the hydrographer's estimations (α & β) under sea-going conditions.

Question 2. To this large and multiple question I have little to add to what I said earlier.

So far as it relates to marine food fishes there is almost no experimental work which would justify an attempt to answer it.

Generalisation from results on fresh water fishes—or from field observations on salmonids (on which I have also worked)—is felt to be inappropriate here.

Finally, may I make one general point.

In considering these problems as a whole, I have been struck by the complete absence of accurate, compendious studies of the normal behaviour of even our commonest food fishes. They do not, of course, stand alone in this respect.

But I believe that the preparation of such monographs—based on direct observation and laboratory experiment—would be a most valuable training to young marine biologists. It would certainly produce facts—and very likely also new ideas.

The views of the meeting, especially on this final point, would be appreciated.

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3.

The Influence of the Gas Content of Sea Water on Fish and Fish Larvae.

By

Eva Henly

At Flødevigen Sea-Fish Hatchery we have, during the last few years, been dealing with the factors which may cause the great mortality of fish eggs and larvae in the sea. We have also tried to find the conditions which are most advantageous for marine eggs and larvae in the laboratory. During this work it has become apparent that the gas content in the sea water may be of great importance for the larvae.

In our experiments we have regularly used larvae of cod, herring, and plaice. These species are among our most common food fishes, and they do represent both the physoclist and the physostome fishes, and also those that do not possess a functioning air-bladder.

We have several times observed in the laboratory that if the gas concentration in the sea water becomes high, the mortality will increase. The problem has been to determine the cause of the "gas disease", and to prevent it.

By using a sand-filter we were able to remove considerable quantities of gases from the water, and the conditions became somewhat better. The gas absorbed by the sand was analysed, and found to consist of 22.5 % oxygen, the rest being nitrogen and other inert gases. In this way both oxygen and nitrogen were removed. It is thus impossible to state which gas may cause the "gas disease". But taking the function of the air-bladder of adult fishes into consideration, the oxygen concentration must be regarded as a very important factor.

All atmospheric gases are found in solution in sea water. In addition to nitrogen and oxygen, the most abundant gases in the air, carbon dioxide is present in large quantities, chiefly as carbonates and bicarbonates. In the absence of dissolved oxygen, hydrogen sulphide may be present.

The dissolved oxygen in the sea water normally varies between zero and 8.5 ml./L, although in areas of intense photosynthesis, the content may exceed this upper limit. We have thus sometimes during the spring found more than 20 ml./L in a sea-water pond where the plankton content was extremely high. Under this condition we have also proved the sea water to contain some peroxides. Nitrogen, which is apparently unaffected by biological processes, varies between 8.4 and 14.5 ml./L. The total carbon dioxide in oceanic waters varies between about 34 and 56 ml./L. The distribution of dissolved gases in the ocean is controlled by the following factors: 1) temperature and salinity; 2) biological activity; and 3) currents and mixing processes.

Water in contact with the atmosphere will tend to reach equilibrium either by giving up or absorbing the individual gases until the water is just saturated. Although the zone of contact is a very thin one, convective movements due to cooling, evaporation, or wind action may bring a layer of considerable thickness into equilibrium with the atmosphere. Some of the oxygen may originate from biological processes, but these too take place in the upper part of the ocean. The oxygen in the deep water thus originates from the upper layers, being brought down by mixing processes.

If newly hatched cod larvae (0—7 days old) are kept in an aquarium without water renewal for half a day, and some fresh sea water of the same temperature and salinity is added, minute gas bubbles will become attached to the larvae which develop white spots and curl up and die. This new water has evidently too much gas for the cod larvae.

Even older cod larvae are susceptible to an unfavourable gas concentration. In particular 3—6 weeks old cod fry are apt to get a "gas disease". At first the air-bladder expands due to excess of gas. The fry then try to get down towards greater water pressure. The aquaria are, however, usually too shallow, and the fry are forced to stay in a layer where the pressure evidently is too low in relation to the gas content in the bladder. The air-bladders continue to expand, and after a few days they have become so big that

the fry float helplessly at the surface, sometimes swimming on their sides and, in severe cases, belly upwards. Their air-bladders become bigger and bigger, and may hinder vital functions. Their jaws are widely separated and the fry refuse to take any food. If nothing is done, the mortality is total. Whether the prime cause of death is choking, starvation, or some other phenomena is unknown.

If such codlings are enclosed in an aquarium provided with a silk net on the top, and lowered in the sea to 2—5 m., the air-bladders by the next day have become normal and the codlings are again able to swim in an ordinary manner. The air-bladders function normally. The same will occur if we put cod fry with expanded air-bladders in a relatively deep aquarium. We have used a cylinder of perspex, 2 m. high, and with a diameter of 13 cm. The fry, affected in a reasonable degree, immediately seek the bottom and swim actively. A depth of 2 m., however, is evidently not sufficient. The fry try to get further down, but stop against the sand on the bottom. Some of the codlings, too much affected, do not succeed; when they get half way they can get no further; they float up again, and after a while they are found dead at the surface.

In nature, when the larva-net, used for pelagic fishing, is hauled from 10—20 m. depths to the surface, the opposite phenomenon may occur although it has only been observed in fishes with a closed air-bladder. Some of the larvae turn belly upwards and come to the surface when transferred to a glass vessel with sea water. The gas in the air-bladder expands.

As soon as the yolk-sack is resorbed the cod larvae will respond to changes in water pressure. If they are kept under pressure say, 5 m. of sea water, they will swim mainly in the upper part of the aquarium. When this pressure is suddenly released, the larvae will sink towards the bottom.

Several years ago cod larvae were reared in our salt water pond (34 × 22 × 4 m.) with remarkably good results, and gas disease was not observed.

The experiments just described apply only to larvae of fishes with a closed air-bladder. Larvae of physostome fishes will respond in a somewhat different way when reared in sea water direct from the reservoir. The mortality may be great, but the clinical picture is different. The gas bubbles are formed in the intestines. When the water comes into contact with the mucous membrane of for instance the herring either in the mouth, the gills, or the intestines, some gas will apparently be liberated. This may probably be explained as a catalytic process. The herring larvae cannot get rid of these gas bubbles and will sooner or later die from obstruction. This year, however, we have prevented the gas formation in herring by rearing the larvae in a greater and deeper aquarium. It may be that the great surface permits the excess air to escape.

Regarding the larvae of fishes without a functioning air-bladder, the clinical picture appears to be almost the same. Larvae of plaice, for instance, respond in the same way as the herring larvae do. Here too we find gas bubbles in the intestines, but the plaice larvae are able to get rid of the gas through the anus, without apparent harm. The plaice larvae may, however, be killed in another way if the gas content is too high.

Two years ago we had a great mortality among young flatfish—a cross-breed between *Pl. microcephalus* (female) and *Pl. flesus* (male). They had been reared in a small aquarium for 3 months and the water had always been filtered before entering the aquarium. Then they were transferred to a larger aquarium supplied with unfiltered water. They thrived for about 1 month, and then the water supply was increased. From then on the larvae died in great numbers. By dissection, it was shown that there were rows of small gas bubbles along the basis of the fin rays of the dead larvae. The tissues were not injured, so the air cannot have been sucked in from bubbles attached to the surface of the larvae; it must have been liberated in the blood. There were also a great number, more or less affected, near the surface, and they showed the same symptoms. The blood circulation in the anal and dorsal fins was very slow, but somewhat better in the tail fin. Otherwise they showed no particular sign of disease.

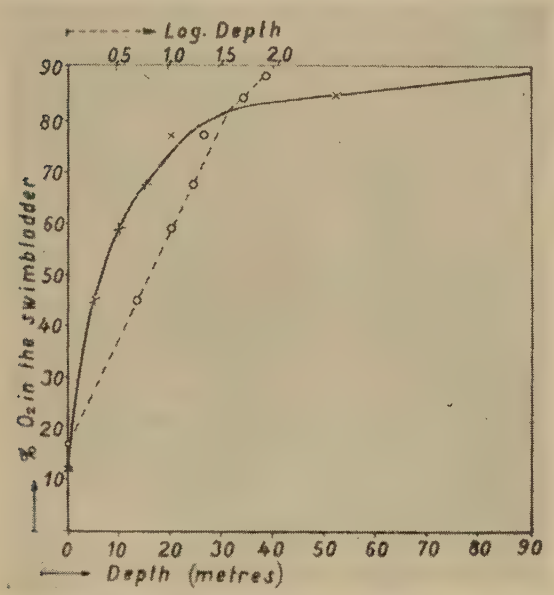
Gas bubbles are often observed on the fins and gills. If there are any injuries on the fins and gills the gas will invade the veins and the fish will suffer from gas embolism. In some cases we have proved that when the oxygen content in sea water becomes extremely high a small amount of peroxide is formed. Some plaice, 3 months old, were kept in sea water containing a little hydrogen peroxide and all died within 2 hours. Minute gas bubbles appeared immediately on the body surface, particularly on the fins, the gills, and the head. The bubbles increased rapidly in size and within half an hour they almost enveloped the whole fish. Some of the larvae had injuries on the fins, and on these places the amount of gas formed was extremely large. After a while the gas was sucked in near the basis of the fins up to the backbone and alongside it. The plaice larvae showed an increased rate of respiration and collapsed.

Not only fish larvae are dependent on a normal gas content in the sea water; there is a great mortality also among oyster larvae if the oxygen content becomes too high.

The difficulties mentioned in connection with the gas content of the sea water have lately been avoided to a certain degree at the Flødevigen Sea-Fish Hatchery, as we now filter the water twice through sand-filters. The oxygen content is in this way reduced by about 20 %. The oxygen content in the reservoir may be, for instance, 114 %. After it has passed filter No. 1 it falls to 102.5 %, and when it is entering the aquaria the concentration is 95 %. Whether this gas removal is a purely physical process, or whether the sand may act as a catalyst, being able to catalyse the liberation of gases from the water, is unknown. But if some iron is present in the sand

the oxygen liberation is greatly increased. This gas removal by means of the sand-filters has resulted in a great improvement, but the difficulties have not been entirely overcome, at least not for the rearing of cod larvae.

Plaice and other flat fishes (including the cross-breed) are now reared in great numbers at the Fløde-vigen Sea-Fish Hatchery without trouble. Plaice and soles have been hatched and kept in aquaria till they are more than three years old. Herring have been kept



The figures show the relation between the oxygen content in the air bladder and the depth.

for two years. We have also succeeded in rearing mackerel up to considerable sizes, but here canibalism is an interfering factor. Rearing of cod larvae has been successful for the first three weeks after hatching, but then the "gas disease" appears, and the mortality between 3 and 6 weeks is much too great, although reduction of the oxygen content has improved the results somewhat.

There is another factor that probably affects the survival of cod larvae in the laboratory, this is their heredity. If the parents originate from the littoral region the chance for the larvae to survive will probably be greater than if the parents are accustomed to deep water. This problem will be further investigated next year.

Pelagic fish larvae are usually found in nature at greater depth than expected. In the laboratory pelagic cod larvae are buoyant in sea water of specific gravity about 1.022. In nature, however, they are found in water of a far higher specific gravity. They are found at a depth of 10—20 m. The depth (water pressure?) is apparently of the greatest importance.

Pelagic fish larvae will, like other forms of zooplankton, avoid places where the phytoplankton concentration is great. It is reasonable to assume that the cause might be a too great oxygen content produced by the phytoplankton. We must of course consider that there may be some antibiotic compounds produced by the phytoplankton that may keep the zooplankton away.

We have carried out some analyses of the air-bladders of cod. We found that cod caught near the surface have an oxygen content in the air-bladder of about 10 %, whereas fish caught at a depth of 25 m. contained 80 % oxygen, and at 100 m. 90 %.

During the last 50 years a rather extensive literature has been produced concerning the gas disease. The symptoms are always the same; as to the cause the opinions diverge. Marsh & Gorham (Washington 1905) described gas disease among larvae and several adult marine fishes very accurately. They came to the conclusion "that nitrogen excess is more important than oxygen excess, and can singly cause the disease process". Semper (abstract) described how he watched sticklebacks, white fishes, and axolotls succumbing when the animals were kept in water rich in gas. He observed gas liberation in the veins and the muscles. Roth (Stuttgart 1922) explained how a great mortality occurred when the water contained a great amount of finely suspended air (because of leaky pumps which began to suck air). The air was liberated into the water as minute air bubbles. Some eels showed a very characteristic clinical response. Their skin became unevenly swollen and the epithelium was penetrated by small shiny air-bubbles. Gudgeon, gold-fish and minnows also succumbed. The author did not state whether the air that penetrated the muscles originated from small air-bubbles present in the water or from dissolved air liberated in the body. But according to his experience the gas disease only occurs when finely suspended air is present in the water. Plehn (abstract 1922) has often found trout with gas disease in sunlit ponds with great photosynthesis. She also described the symptoms, and they fully agree with those found here in the case of plaice larvae. She stated the cause of death to be gas embolism. The larvae would survive, she said, if the fishes were transferred to normal water. Haempel (abstract 1937) has proved (using young salmonids) that an increased oxygen content at first causes dyspnoea (difficulty of breathing), after which the respiration stop (apnoea). A secretion of slime together with great sensibility follows, and finally a spasm (caused by oxygen narcosis) occurs, so that the fish choke. Mršic (abstract 1933) described a very interesting case of gas disease (and hopes to prove the cause to have been a supersaturation with carbon dioxide). All fishes living in the water reservoir of Zagreb were attacked by the gas disease. Trout larvae were transplanted, but these also died. When, however, the water was aerated, the fishes survived. Mršic was convinced that the cause was a supersaturation with carbon dioxide.

Thus several theories have been put forward as to the cause of the disease. The most important are oxygen excess, nitrogen excess, carbon dioxide excess, pH variations, temperature variations, and irritations from associated plants, or compounds liberated from the plants, or the effect of two or more of these factors.

At Flødevigen Sea-Fish Hatchery we assume the main trouble to originate from: 1) the oxygen concentration; 2) the water pressure. It is uncertain if these factors may be of importance in nature. It appears reasonable to expect, however, that if newly hatched larvae are brought into contact with sea water containing a high amount of oxygen, they will be seriously affected. Further, if young individuals of physoclist species, at the age when the air-bladder is formed, are brought from 10—20 m. by the current to the surface, a gas disease will occur.

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The Relation of Plankton Research to Fisheries Hydrography.

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The sea is ever on the move. For many years we have known from the work of the hydrographers the general outlines of the circulation of the waters of the North Sea and neighbouring regions. But it is only in the years since 1920 that we have been able to superimpose upon this generalized picture an impression of the planktonic populations inhabiting the moving waters. We can now visualize in some degree of detail the types of organisms, both plant and animal, likely to be present under certain conditions in any one area and the changes that might take place in these communities in the course of time as they drift about. Moving water masses are no longer to our minds merely volumes of sea water of certain salinities and temperatures; they are very much alive and have a biological history which itself affects the chemical nature of the water.

Such, no doubt, was also the type of picture in the minds of earlier workers like Cleve and Gran at the opening of this century, but the picture is certainly much more detailed for us now.

It is thus no longer possible to relate purely hydrographical, or physical and chemical, characteristics of sea water to the fishes' behaviour without taking into consideration the living organisms in that sea water. Though many apparent correlations may be found between the fisheries and the physical and chemical conditions in the sea, the real relation will often be between the fish and the plankton in the water. In other words the plankton will mediate between the potentialities of the water and the fish.

In this selective review I propose first to consider how the study of plankton can help to give information of direct value to the fisherman, and second, the significance of the intermediary position that plankton organisms hold between the fish and the surrounding hydrographic conditions—somewhat arbitrary divisions which, as will soon be seen, are to a certain extent interdependent and difficult to disentangle.

In either aspect we must bear in mind the fundamental division of fishes into pelagic, mainly plankton-eating, fish which live largely in the water masses moving above the bottom; and demersal, chiefly bottom-living, fish which frequent areas over which different water masses may move. The young pelagic stages of both types of fish belong to a third category, for they are themselves planktonic.

It is also necessary to realize that the success or failure of a fishery may be due either to changes in the habits and distribution of the fish themselves, or to fluctuations in the abundance of year-classes of the fish. In either instance the plankton may be a determining factor.

Direct Effects of Plankton on Fishing.

1. Relation of Catches to Plankton.

(a) Favourable Organisms.

After obtaining the necessary information on the relative values of the different plankton organisms as food for the fish, observations can be made to see whether the best catches of the fish coincide with the areas in which the most important food species are most abundant. It is, perhaps, unnecessary to state that this should only be done for fisheries for the fish when it is feeding, and not when it may have ceased to feed preparatory to spawning.

A great deal of information has now been published on the food of the more important pelagic fish (e. g. Hardy, 1924; Jespersen, 1932, 1944; Savage, 1931, 1937). With this knowledge in mind A. C. Hardy inaugurated large scale observations by the fishermen with indicator discs to see whether the best catches of herring were related to the abundance of the most important food organism, *Calanus*. The results showed a positive correlation (Hardy, Lucas & Henderson, 1936). It appeared that by selecting the water rich in *Calanus* in which to fish a gain of some 20 % might be made over the catch secured by fishing at random.

The full story is not yet told, for extensive investigations are still being carried on by the plankton laboratory of the Scottish Marine Biological Association in Edinburgh.

(b) Unfavourable Organisms.

As a result of the above investigation there was also definite evidence that the presence of some kinds of plankton organisms was unfavourable to fishing (Henderson, Lucas & Fraser, 1936). In fact areas in which *Phaeocystis* and *Rhizosolenia* occurred were long ago shown by Pearcey to give poor catches compared with areas in which there was plenty of copepod food. Similarly the occurrence of small "jellyfish" was found to be correlated with poor catches of herring (Lucas & Henderson, 1936).

Previous literature on the subject is given by the above authors and it is unnecessary to mention more here. More recently, however, Steven (1949) has shown a correlation between good catches of mackerel and the occurrence of patches of "yellow water" due to copepods, and concluded that within limits "since mackerel congregate in the yellow patches, the more numerous those patches are in any year and the greater their extent, the more favourable are the chances of their being found and fished in, with consequent benefit to the commercial fishery." He thus explained the previous finding of Allen (1909) that the catches in May were somehow affected by the amount of sunshine earlier in the year, since in years with favourable light conditions there might be expected to be a rich phytoplankton crop leading to good survival of copepods.

2. Relation of Catches to Type of Water.

Having found the most prevalent food and shown a correlation between the catches of fish and the distribution of the food, a survey can be made of the composition of the plankton community in the area. It may be found that there are a number of species which appear to characterize the plankton and distinguish it from plankton communities in other areas. In this way the type of water in which the fish are finding their best feeding may be labelled by such indicator organisms and its hydrographical features examined. Many such indicators are in fact now well known (Russell, 1939), and the mere presence of these indicators, apart from the presence of food, may tell the fisherman if he is in the right type of water in which to search for the fish.

This could perhaps prove of value in guiding a whole fleet to that area in which there is the best chance of finding good fishing. There are in fact indications that the herring in certain areas prefer at times the mixed oceanic and coastal waters characterized by *Sagitta elegans* and about which the picture is becoming more clearly defined. In fact, our whole knowledge of plankton indicators in the North Sea and Atlantic is being immensely increased at the present time by the workers at the plankton laboratory in Edinburgh using the Hardy continuous plankton recorder (see e. g. Lucas & Stubbings, 1948; Marshall, 1948; Rae & Rees, 1947; and Rees, 1949). From the point of view of fisheries hydrography the importance of their research can hardly be overestimated.

It is quite unknown whether the fish are attracted to the type of water by chemical and physical conditions, or the "taste" of the water, or whether they find it by random movement and are held in the area by the supply of food. For instance Wood (1937) says: "When food has been located in abundance, one expects that the herring will naturally remain within the food-bearing mass as long as there is the need or desire for food, so that the movements of the herring are controlled for a time by the drift of the organisms on which they feed."—"It is desirable that the study of the distribution of herring food organisms should be intensified, to correlate with and to supplement the analysis of the movements of the herring shoals . . . , and to help in the elucidation of movements of which we are still ignorant."—"The normal abundance of food in the northern North Sea during spring and early summer is obviously an inducement for the shoals of different stocks and races to concentrate in northern waters. In July, when the need for food is less acute than in the spring, and when food organisms become more widely distributed throughout the North Sea, the components of each stock undertake independent movements, tending in the case of autumn spawners in the direction of their spawning places."

Another great feeding area for the herring, the principal feeding ground in English waters, is in the Shields area off the north-east coast. Savage (1937) showed that very favourable feeding conditions in that area in 1931 were reflected in good catches, and he concluded that a rich supply of *Calanus* early in the season attracts the herring to this feeding ground. Conversely, Jensen (1947) correlated poor catches of herring in the Bornholm fishery in the Baltic in 1939 with a poor supply of copepods.

As I have said, it is not known whether it is the type of water or the food that first attracts, but the Shields area is one in which the influence of the mixed oceanic and coastal waters is felt, and Burton & Meek (1932) have shown a relation between the occurrence of *Sagitta elegans* and S. *setosa*, and the herring.

A similar relation has been noted in the English Channel in the neighbourhood of Plymouth. The herring ceased to come when the *Sagitta elegans* plankton was replaced by that of *S. setosa*. But in this instance the herring are spawning, and, although Lebour (1924) has shown that at the same time they may feed, the attraction should be the spawning ground. It could, however, be that when the whole area is filled with *Sagitta elegans* water the herring are already well up-Channel feeding, and they then move in towards the coast to spawn. But when *Sagitta setosa* predominates the herring are altogether absent from the area.

It should be realized that water is continually passing in and out of and circulating around the North

Sea, so that in time the whole body of water is renewed. But many of the herring probably stay within the North Sea area all their lives. In it they make circulatory migrations, leaving the estuaries and coastal areas of their youth and making their way to the feeding areas. They must then follow these feeding areas around until they are mature and once more make inshore or seek out those fixed localities in which the bottom suitable for spawning has always been found. Little is known of the rate of movement of pelagic fish. Bullen (1912) records that a mackerel shoal moved 33 miles in 9 days, presumably drifting with the water mass as they made circulatory feeding movements; in contrast he quotes Mathias Dunn as stating that pilchard on migration move at 1.5 miles an hour. Thus while the seeking of the spawning area is probably directional and deliberate, the movements during feeding are probably controlled by the distribution of the food. It is thus possible that, while feeding, the chemical and physical properties of the water have little effect on the fishes' movements, and that the situation of their customary spawning grounds in relation to their last prespawning feeding area may have been determined by the distribution, abundance and drift of their food supply. The chief factor in the latter is the translation of water bodies by currents, winds and oceanic influences (cf. also the distribution of herring and *Calanus* off the north coast of Iceland, Steemann Nielsen, 1935, p. 72).

3. The Influence of Plankton on Non-Feeding Fish.

When the herring are ceasing or have ceased to feed and are actively migrating to their spawning grounds the plankton may still play a part which will affect the fishermen. While it has already been mentioned that the presence of certain planktonic organisms are unfavourable to fishing, certain of these organisms when present in great quantities over extensive areas appear to form actual barriers to migrating fish. The classic observations from the Lowestoft laboratory have shown the effects of phytoplankton patches on the East Anglian fishery (Savage, 1932; Savage & Hardy, 1935; Savage & Wimpenny, 1936; and Graham, 1398). In this connexion the most effective organism is *Phaeocystis*. Thus, while the general hydrographic conditions of the water may be quite favourable for the herring's migration the plankton intervenes.

It has been suggested (Savage & Wimpenny, 1936) that the herring tend to mass against the edge of a phytoplankton patch. This appears worth following up since there is an indication that the spawning area of the mackerel in the western Celtic Sea (Corbin, 1947) coincides with the area of greatest phytoplankton development (Mare, 1940). Of similar interest is the occurrence of eggs and young of zooplankton in phytoplankton patches recorded by Wimpenny (1937), to which added significance is given by the work of Marshall & Orr (1952) on the influence of feeding on egg-laying in *Calanus*.

4. Plankton and Recovering Spent Fish.

After spawning in the eastern end of the Channel the recovering herring probably drift for a time up the French and Belgian coasts in normal years. At this time they are beginning to feed again. Savage (1932) and Carruthers (1938) have shown that the influence of the wind might lead to a redistribution of the copepod swarms on which the fish are then feeding. Prolonged easterly winds would tend to drift the copepod swarms away from the continent towards the English coast, and hold up the drift from the English Channel along the French and Belgian coasts.

5. Effects of Plankton on Condition of Fish.

The quantity and nature of the available food will determine the quality of the fish feeding thereon. Wimpenny (1938) showed that there are seasonal variations in the fat content of the plankton and that the herring are at their fattest the month following the period when the amount of fat in the plankton is greatest. As a result of observations in the region of Flamborough Head over a number of years Wimpenny (1944) has also shown that there are annual variations in the amount of fat in the plankton. These annual changes are undoubtedly due to hydrographic conditions; for instance the copepods in *S. elegans* water appear to contain more fat than those in *S. setosa* water (Russell, 1936 a). Recently Wimpenny (1950) and Hodgson (1950) have reported an indication that the quality of the herring each year is correlated with the fatness of the plankton. A similar correlation has been reported by Jensen (1947) from the Baltic.

Later Jensen (1950) correlated yearly variations in the fat content of herring of similar stages of maturity in Danish waters with the degree of influx of water of high salinity, which would presumably carry with it more nutrients and be more fertile for the production of planktonic food.

It is well known that fishes exhibit differences in growth from year to year which must be conditioned to a large extent by the food supply. Thus Andersson (1938, 1943 and 1947) and Molander (1943) have assumed a connexion between variations in growth and supply of planktonic food in the confined waters of the Baltic. With a relatively constant supply of food the amount of growth will vary inversely with the size of the fish population; the best year-classes will thus show the poorest growth. I am not aware of any recorded evidence of increased growth occurring in years of rich food supply in more open waters; it might have been expected that the effects of the abundance of food in the Shields area in 1931 will have shown on the herrings' scales.

Oscar Sund (1943) suggested also that scarcity of food might possibly be responsible for delayed maturity in herring in Norwegian waters.

Plankton and Hydrography.

The composition and abundance of a plankton population is controlled by the nature of the water in which it lives.

In the earlier years of fishery research it was customary to record the two characteristics of sea water, temperature and salinity—valuable guides to the origin and circulation of the water. These being the known factors of the environment there was perhaps a natural tendency to try and correlate the distribution of the living organisms with these two characteristics. Later, attention was turned to measuring those properties of the water which showed changes effected by the living organisms, such as pH, oxygen concentration, silicon and the nutrient salts of phosphorus and nitrogen. The latter characteristics are important from the point of view of the fertility of the water.

It seems hardly necessary to dwell at length on the importance of nutrients for plankton organisms or the implications of water movements and upwelling of rich water from the ocean depths. There are, however, certain aspects which should be discussed.

Harvey (see Armstrong & Harvey, 1950) has recently made possible a considerable advance in knowledge by the improvement of a method for estimating the total phosphorus content of the water. It should now be possible to find the life-bearing potentialities of a water at any time of year, instead of only at the periods when all the phosphorus has been returned to the water in a soluble form.

But the fishery potentialities of a water mass, namely its power to attract fish by abundant food supply, or its possibilities for survival of maximal numbers of young fish, cannot be expected to be determined entirely by the amount of nutrient substances initially available. There are many factors which intervene to obstruct or divert the straightforward course of events.

Before considering these factors, many of them hydrographical in nature, mention should be made of results which have established a direct relation between the potential fertility of the water and the survival of young fish.

For a period of sixteen consecutive years, 1924 to 1939, and four years since the war regular collections have been made off Plymouth with a stramin ring-trawl. The results have undoubtedly shown a correlation between the total number of young fish in the plankton and the maximum phosphate values of the previous winter (Russell, 1939). It has also been established that the rich years are characterized by the presence of mixed oceanic and coastal water in the area indicated by the occurrence of *Sagitta elegans*. In these observations the results were found to apply to all species of fish present in the collections.

Poulsen (1944) has reviewed the results of his comprehensive series of observations on the occurrence of young cod in the plankton in Danish waters over the same period, 1923 to 1939. He found a correlation between the number of young cod in the ring-trawl catches in April and May, and the quantity of plankton in the months January, February and March. He demonstrated an agreement between fluctuations in numbers of larvae and the older fish; "in other words that the frequency of a year-class and, accordingly, its effect on the size of the stock of cod is determined already at the larval stage."

Johansen (1927) had earlier shown a correlation between the abundance of young plaice and the temperature and salinity of the water in the years 1904 to 1926. He suggested that "in cold winters, when there is a relatively marked outflow of comparatively fresh water from the Baltic through the Belts and the southern Kattegat, the tiny plaice larvae fail to obtain sufficient nourishment, and die of starvation *en masse*."

"If future investigations should confirm the hypothesis that between the quantity of plankton and the number of young plaice there is a connexion even approximately as close as Fig. 6 indicates, it will be possible to form a basis for estimating in advance the yield of the fishery more easily and cheaply by collecting plankton than from fishing experiments for young plaice. The quantitative plankton investigations should naturally be connected with researches as to what kind of plankton the tiny plaice larvae preferably feed on."

The inference seems justified that water rich in phosphorus gives rise to an abundant plankton and hence a good survival of the young of those fish spawning in the area. However, rich water cannot necessarily be said always to lead to a good survival, for in one of the years of the Plymouth observations, 1929, when there was fertile water in the area the usual peak of young of spring spawning fish was missing. It was possible on that occasion to link this scarcity of young fish with a great abundance at the time of voracious ctenophores (Russell, 1935, p. 166).

The survival of young fish will thus obviously be liable to the normal biological hazards of predation and disease. In the latter respect Cattley (1948) records parasitic castration on a wide scale in the copepod *Pseudocalanus* which might have serious effects on the abundance of this important food organism.

But there are other factors which may interfere in the production of good survival of young fish in potentially rich water. A number of these have been reviewed by Steemann Nielsen (1935, pp. 42 and 71). Among the biological factors one of the most important is obviously the timing of the succession of species in the plankton. The work of Soleim (1942) on herring larvae and Wiborg (1948) on cod larvae has confirmed Hjort's theory of the need for a supply of the right food organism at the right time.

The regulation of the plankton sequence is controlled partly by hydrographic conditions. Of great importance in this respect is the degree of stability or turbulence of the water with its attendant effects of

turbidity and reduction in light penetration (e. g. Steemann Nielsen, 1943, for the south coast of Iceland). But apart from the effects on phytoplankton production, turbulence may have direct or indirect effects upon the animal life. Huntsman & Reid (1921) have shown that *Sagitta elegans* and other animals with planktonic eggs appear to be unsuccessful in their reproduction in the turbulent waters of the Bay of Fundy. They attributed this to low temperatures resulting from turbulence, but Gran & Braarud (1935) later showed that the phytoplankton production was reduced, which may limit the food supply for plankton animals. Similar conditions perhaps result in the low plankton content of the eastern end of the English Channel.

It can thus be realized that although the water may be potentially rich there can still be much fluctuation in the successful survival of young fish from complete failure to great production. It would appear that, by contrast with the Bay of Fundy, the most favourable circumstances possible exist in the Kattegat, where nutrient-rich water is continually being brought from the deeper layers to the surface and remains completely available to the plankton organisms since its stability cannot be broken down by the wind (Steemann Nielsen, 1940).

It would be interesting to know the relation between the quantity of available phosphorus and the survival of young fish. The extreme variation in the quantity of phosphorus over the long series of observations off Plymouth was less than three times. But the variation in abundance of all young fish excluding clupeids has been much greater, amounting to sixteen times. The variations for individual species were even greater; similarly Poulsen (1944) found a variation of about fifty times for the cod.

The total production of any one year's brood will depend not only on the amount of phosphorus in unit volume of water, but also on the actual total volume of that type of water available for transport of eggs and developing larvae, provided that the act of spawning of the adult fish population is not instantaneous. Thus, it will be evident that a larger incursion of favourable water into the northern North Sea should supply a greater total of young haddock than a smaller one.

There might also be a differential selectivity of different species of fish, some developing at the expense of others. It is, therefore, desirable to know whether fish with similar distributions and breeding periods fluctuate in step. In general, off Plymouth, all fish appeared to fluctuate together.

There might be considerable fluctuations in the supply of critical food organisms. Wiborg (1948) gives figures of 10—20 cod larvae per cubic metre to 5,000 to 25,000 food organisms of the right size in the same volume of water. Both he and Soleim (1942) have recorded large numbers of dead cod and herring larvae, respectively, coinciding with scarcity of food organisms. Wiborg's results showed that the numbers of food organisms for young cod in comparable catches ranged between 860 and 26,200.

The difference between the range of phosphorus variation and that of the total number of young fish off Plymouth was not restricted to young fish; it appeared to hold for all the larger predatory carnivorous animals in the plankton. For instance, the total number of medusae in *Sagitta elegans* water was many times greater than in *S. setosa* water (Russell, 1938). Similar differences were shown between these two types of water off the mouth of the English Channel, though the numbers of small herbivorous copepods did not vary so widely (Russell, 1936 a).

The success in survival of predators like young fish must depend upon the dispersal of their food organisms, and their chances and ability for catching them. Thus, there may be a threshold value of dispersal below which the young fish will starve. A two fold increase in the number of food organisms would greatly increase the chances of survival. Information of the type of that secured by Wiborg (1948) giving the numbers of cod larvae of different stages in relation to the numbers of suitable food organisms is much to be desired.

It may also be that for some organisms there are other unknown factors. For many years research workers have postulated the presence or absence of undefined substances to explain the differing planktonic populations of oceanic and varying types of coastal waters (e. g. more recently Fraser, 1939; and Clarke, Pierce & Bumpus, 1943, p. 223). The evidence has been ably reviewed by Lucas (1947), who has stressed the probable importance of different metabolites which must be present in the sea.

As yet no specific substance has been isolated and its effects shown for the animal plankton. But Wilson (1951) has now shown for the first time that natural offshore waters, well away from immediate land pollution, differ in their capacities for supplying a suitable environment for the development of larval stages of bottom invertebrates. In this instance he found that the larvae of an echinoderm and two polychaete worms developed in a normal manner in water collected from the Celtic Sea, but were abnormal and unhealthy in water collected from mid-Channel. The Celtic Sea water was probably mixed oceanic and coastal water of the type characterized by a large population of *Sagitta elegans* on both sides of the Atlantic.

It is easy to realize how all these factors we have been considering may play a part also in the lives of the demersal fishes living on the bottom. Rich overlying water will supply favourable conditions for the survival of larger numbers of larval stages of bottom animals which will enrich the bottom feeding grounds when they settle. It will in addition supply more food for the filter feeding organisms, resulting in their more rapid growth. Thus the varying hydrographic conditions may have a considerable effect, through the plankton, on the growth of bottom feeding fish. Blegvad (1927) has shown for instance that the presence of high salinity bottom water in Danish seas is favourable for the production of young plaice.

Quantitative observations over large areas of the sea bottom have not been made, but it may be expected that the abundance of life would be greatest in those areas which are overlain by *S. elegans* water for the longest periods (Russell, 1936 b; Cooper, 1948). Variations in the quantity of bottom animals must be largely affected by movements of overlying water. Jensen (1943) in fact recorded a correlation between the growth of plaice in 1938 and 1939, and the amount of available food in the Horn's Reef area.

In conclusion it may be remarked that while our knowledge of conditions in the sea has now advanced to such a degree that we can realize more clearly the possible causes of fluctuations of year-classes of fish, we still lack concrete evidence. There are now correlations known to fit wind and water movements, but the success of any one year-class of a fish has not yet been pinned to the abundance of the right food at the right moment, or even the recorded destruction of eggs and larvae by storm action. It should be one of the aims of plankton research to attempt, by observations over a number of years, to correlate the numbers of survivors of a year-class of fish with the presence or absence of any one or more types of plankton organisms during the early planktonic life of the fish. Soleim (1942) and Wiborg (1948) have shown this to be possible. These results should be related to the hydrographical conditions.

It is quite evident that many correlations between the fisheries and hydrographical conditions will not be fully explained without simultaneous knowledge on the plankton.

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5.

The Application of Studies on Estuarine Hydrology to Certain Problems in Australian Oyster Biology.

By

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For the last ten years the C.S.I.R.O. Division of Fisheries has been conducting investigations into the hydrology of Australian estuaries. Economically these shallow brackish water regions are important to the Australian fishery. Both the mullets, which are still a major Australian fishery, and the Sydney rock oyster, inhabit these estuarine waters for the greater part of their life cycle.

Moreover the possibilities of pisciculture in the brackish waters, of enclosed swamps and pools, are of great importance to protein starved areas like the Mandated territory of New Guinea and to many of the Asiatic countries in general. It is understandable therefore that much research effort has been expended by the Fisheries Division on a programme of hydrological investigation designed to solve problems concerning the ecology and productivity of this region.

In a recent publication in the *Australian Journal of Marine and Freshwater Research* (Vol. 2, No. 1, 1951), the author has reviewed the comparative feature of these studies to date. No attempt, therefore, will be made in this communication to give a detailed account of the work but only a brief statement on some practical possibilities arising out of these studies in the field of oyster cultivation.

In connection with our oyster investigations several problems were of immediate concern. It appeared essential to ascertain the fundamental reasons for the differences in biological behaviour of oyster stocks in different estuaries and in various parts of the same estuary. Thus there were estuaries in which the adult oysters were capable of only poor growth but in which the spat-fall was always consistently good. There were other estuaries in which the adult oysters fattened rapidly but were incapable of self perpetuation because of poor spat-fall. In some rare cases both fattening and good spat-fall occurred in the one estuary. This problem was found to be bound up with the hydrological characterization of the estuary and is treated in the previously mentioned paper. The problem of food supply to the growing oyster was also a principal feature of the investigations.

Soon after our investigations commenced it became apparent that production of phytoplankton, which at that time seemed to be generally accepted overseas as the optimum food for oysters, would always be low in Australian estuaries, chiefly because of an almost complete absence of phosphates in the run off waters of the E. Australian coast, but also because of the turbidity and turbulence of the shallow waters of the oyster fattening areas. After continued examination of the water for phytoplankton had verified this deduction it became necessary to seek within these estuaries other sources of food material to supply the needs of the dense oyster stocks.

Invariably the best oyster fattening grounds were associated with mud-sand intertidal flats in the shallow estuarine zone of an estuary. Chemical examination of these muds showed them to be very rich in phosphates, even in a rather soluble interstitially retained form. Moreover the longitudinal distribution of such phosphates always showed a marked peak at about the zone of fattening with a quite distinct minimum in the sand bottom of the more seaward and poor oyster growing region (Fig. 1). Further study

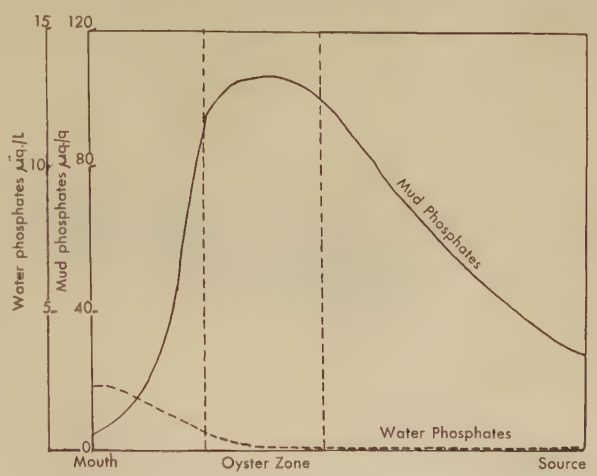

Fig. 1. The longitudinal distribution of available phosphates in the mud and water of the George's River (Botany Bay) estuarine system.

over a period of years seemed to confirm this association and the hypothesis was therefore adduced that the productivity of the waters of the intertidal regions, in which oyster fattening occurs, was governed by the rate and effectiveness of utilization of these mud phosphates by a permanent surface trophic film of bacteria, microprotozoa or sessile diatoms.

In situ processes, probably bacterial, assisted by chemical processes replaced these interstitial phosphates by desorption and degradation of the adsorbed and insoluble phosphates on or within the mud particles. A continuous cycle of phosphate supply and organic production could thus be maintained at the mud surface.

As the mud surface was exposed some 12 hours out of 24 by tidal action, a percentage of the population of micro-organism would be destroyed daily and be swept into the overlaying water as detritus during the high tide phase. Because this organic detrital material is lighter than the sand and silt of the bottom, it would be transported to a higher level by turbulence and thus become separated out from these inorganic elements.

In actual practice tray cultivation of Sydney rock oysters is carried out at a rather precise level, with a lowering or elevation of only about 20 cms. from this level being rather detrimental. The full hypothesis then is that at a certain critical level above the mud surface, the detrital material continually swept off from the bottom mud by turbulence is ingested in relatively pure form by the oysters on the trays.

This detrital material is a product of continual destruction of a micro biota on the mud surface with trophic connections with the nutrients and in particular the interstitial phosphates of the subsurface mud. The cycle is schematically shown in Figure 2. At this stage of the investigations it seemed possible to subject such a hypothesis to an actual field test.

Shell Point is situated within the fattening region of the George's River (Botany Bay) estuarine system

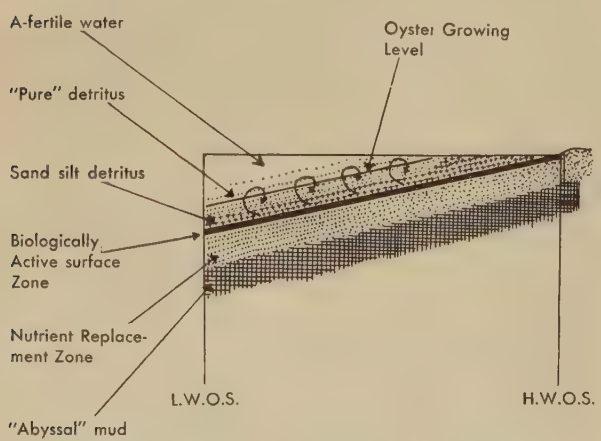

Fig. 2. The probable cycle of organic production on a typical intertidal mud flat of a central New South Wales estuarine system.

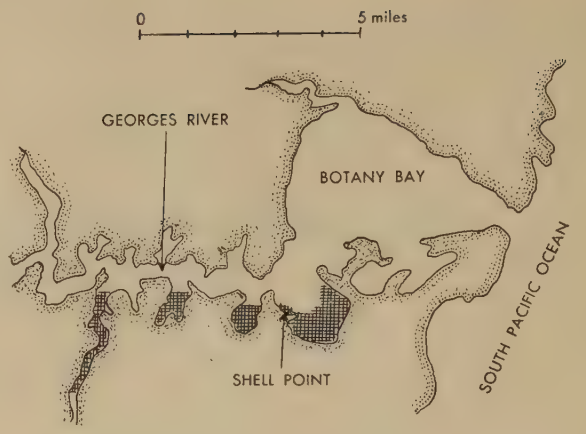

Fig. 3. Map showing the location of the principal oyster growing grounds (cross hatched) and of the experimental site at Shell Point in the George's River (Botany Bay) estuarine system.

(Fig. 3). The growth rate of oysters there is not as rapid as in adjoining areas, nor is the phosphate content of the intertidal muds as high as in these other regions. Could we stimulate the growth-rate of oysters at Shell Point by the addition of phosphatic material to these intertidal muds?

As the phosphate adsorbing power of these muds was considerable the losses by leaching and subsequent transport in the water were not considered a deterrant. At the commencement of a growing season a plot of some 50 square metres was therefore chosen near the low water level of the intertidal region. At low tide a mixture of superphosphate and linseed oil meal distributed at the rate of 5 kilograms per 100 square metres was raked into the surface of the mud. The linseed oil meal was used as a persistent source of nitrogen and carbohydrates for the increased micro biota that the increased phosphates should develop. After about a week when equilibrium had been reached trays of immature oysters were placed over these plots, and also over non-treated control plots some distance away. The growth-rate of these experimental and control oysters were measured for a period of several years. In addition frequent chemical analysis of the muds showed how the phosphate, carbon and nitrogen levels of these muds varied over the period. The general results of this experiment are given in the previously quoted paper and show that mean growth-rate over the experimental was always much greater than that over control plots.

The method of broadcasting fertilizer and raking it into the mud surface seemed rather crude and some attention was given to an alternate method. In the latest series of experiments small plots some 5 square metres in area are chosen and enclosed below the mud surface by wooden boards. The upper six inches of mud is then removed the fertilizer added and the surface mud replaced. These plots are so sited on the intertidal plot that proliferation of the micro biota

on their surface will result in the transport by water movement of detrital material over a large area of the oyster tray cultivation.

By locating the fertilizer at this subsurface level the losses by leaching should be practically negligible whilst the phosphates would still be available for surface utilization. The latest results of this method are particularly encouraging.

The possibility of releasing phosphates from these estuarine muds by mechanical means is also under consideration. In India and Asiatic countries in general the pond fish farmers allow the pond bottom to dry out and fallow, plough it, recover with water and repeat the cycle until the bottom has the right fertility as judged by rather empirical tests. In this way they probably alter chemical conditions in the mud and release nutrient material for utilization by the micro benthos or pond plankton.

In Australia however, as phosphates do not appear to be added to these intertidal muds in any quantity from the water and the oyster stocks return only a small fraction of phosphates to the water before human consumption, the eventual addition of phosphate fertilizers would have to be considered.

6.

Hydro-Biological Correlations at the Entrances to the Northern North Sea in 1947.

By

J. H. Fraser

For some years the work at Aberdeen has included investigations on the "plankton indicator species" and in this the Aberdeen Laboratory has been fortunately placed because of the many and varied ecological conditions that exist in the seas around Scotland: for instance the North Sea, relatively shallow and with water of salinity of about 34.5 ‰; the incoming Atlantic water, warm and of higher salinity; and there is cold boreal water near the surface in the northern area and in deep water off the western seaboard. The interchange of these waters which have different fertilities as well as different temperatures and salinities profoundly affects the ecology of the area, which includes important commercial fisheries. The degree of interchange and the routes followed by incoming water masses has, therefore, long been a subject of hydrographical study and it is being supplemented by hydro-biological investigation.

The year 1947 has been chosen as an example of the kind of relationships that can be used to link the plankton with the hydrographical conditions because in that year there were a number of outstanding hydrographical features. These may be briefly described by reference to the work of several hydrographers as published in the *Annales Biologiques*. Smed (1947 a and b) has divided the area discussed in this paper into three (see Fig. 1), — J (Faroe), K (north coast of Scotland) and F (north-western North Sea); and he has published data of the surface temperature anomalies in these areas which are reproduced here in graphical form as Fig. 2. These although generally speaking positive in relation to the zero line even at the beginning of the year are, when compared to the general high trend since 1932, much lower than usual in spring, but started to rise about May and are very high indeed in July, August and September, especially in area F, where positive anomalies of 2.8° C. were obtained in August. The anomalies fell nearly to normal by the end of the year. Hermann (1949), from observations in July, 1947, argues an inflow into the Faroe-Shetland Channel only in the south-eastern side of the section, and outflow in the north-western side. Tait (1949) states that a small tongue of oceanic water was found immediately north of Shetland but on the rest of the 61° N. line from Shetland to Norway there was no evidence of oceanic inflow into the North Sea. He further suggests that the tongue of water present in the Faroe Channel was blocked by a southern ex-

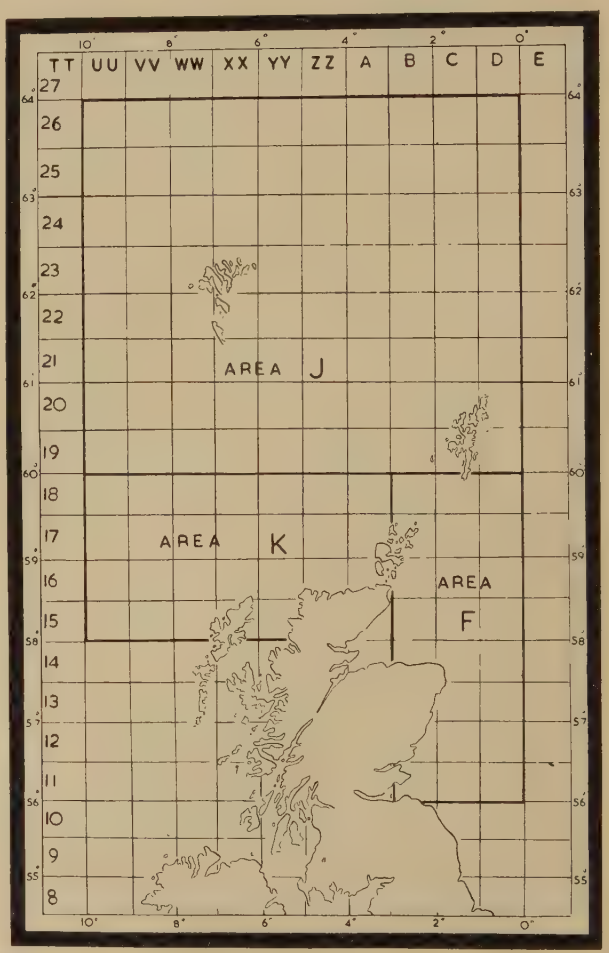

Figure 1. Map showing the areas 'J', 'K' and 'F' as defined by Smed.

tension of the boreal waters from the Norwegian Sea. From July to December only in the north-west corner of the North Sea was the salinity greater than 34.99‰ and he suggests that the high surface temperatures were due to solar radiation, leaving the bottom layers cold, so that the North Sea south of Fair Isle had positive temperature but negative salinity anomalies.

There is thus a picture of a warm oceanic influx entering the Faroe Channel chiefly along its south side, extending northwards close to the Shetland, and only very slightly penetrating the North Sea round the north and east of Shetland, but on the whole being held up by Arctic water so that the normal inflow over the 61° N. line was absent. The North Sea was thus almost completely barred from oceanic influence in spite of a probable normal influx off the western end of the Faroe Channel but, because of intensive solar radiation, the surface of the northern North Sea was almost 3° warmer than usual.

The distribution of plankton indicator species not only fully supports the hydrographers' interpretation but adds details that may be only small in terms of water masses but may nevertheless be of considerable ecological significance.

The Chaetognatha are in themselves a group of useful indicators of most of the conditions found in the Scottish areas, and have been discussed by Fraser (1949 b) and Marshall (1948). In most years when there is a pressure of oceanic water from the north into the North Sea, the mixed oceanic and coastal water, containing *Sagitta elegans*, pushes the North Sea water containing *Sagitta setosa* away from the area east of Shetland, Orkney and Scotland and confines *Sagitta setosa* to approximately south and east of a curved line from the Firth of Forth to the east of the Fladen Ground, as indicated by the dotted line on Figure 3. In 1947, however, the pressure into the North Sea from the north was absent and *Sagitta setosa* was found much further north and west than usual (Fig. 3). *Sagitta setosa* was present on the 61° N. line between Shetland and Norway at about 2° E. but was absent in the north-west corner where Tait described the presence of a tongue of oceanic water and it is significant that the oceanic species *Sagitta lyra* was found to the north-west of Shetland in June.

The presence of boreal waters in the area is shown by the distribution of *Sagitta maxima* and *Eukrohnia hamata* which were found in unusual abundance on both the Faroe-Shetland and Faroe-Hebrides lines, and, in view of Hermann's statement that the inflow was confined to the south side of the Faroe Channel, it is significant that *Sagitta maxima* was not found at the southern stations on the Faroe-Hebrides line. *Sagitta serratodentata*, which was found in the oceanic water outside the North Sea had only succeeded in penetrating to the area east of the Moray Firth in April and May, not by the route via north of Shetland but evidently by a route to the immediate north of Orkney to be recorded in April in C. 17 a, C. 17 d, and D. 17 c, and in May at C. 15 c and D. 15 c. *Sagitta elegans*, normally very abundant off the east Scottish coast, was comparatively scarce there in 1947.

That there was ample evidence of the presence of oceanic water to the south-west of the Faroe Channel is shown by the presence there of an abundance of exotic species including *Sagitta lyra*: the larvae of such fish as *Fierasfer*, *Stomias*, *Paralepis*, *Nansenia* etc.; the pteropods *Clio pyramidata*, *C. cuspidata* and *Diacria trispinosa*; the siphonophores *Physophora*, *Galetta australis*, *Chelophyes appendiculata* and *Lensia concoidea*; *Rhincalanus* and doliolids (Fig. 4). Of these only the less extreme forms such as *Clio pyramidata*, *Physophora*, *Chelophyes*, *Rhincalanus* and doliolids reached the north-west of Shetland and only *Physophora* was found north-east of Shetland in July though *Clio* and *Chelophyes* were found with it over the Norwegian Deeps.

Other indicator species can be used to trace the distribution of the water masses. The doliolids, though not abundant, were in sufficient numbers to illustrate their indicator value. They were taken at the south end only of the Faroe-Hebrides line in June and at the extreme south-east end of the Faroe-Shetland lines, with a single October record to the immediate east of Shetland. They were also taken in the Faroe Channel in August and in the same months were found north of Orkney and east of Pentland. By September they were found distributed over the area south of Fladen and off the east Scottish coast and they continued to be found off the north English coast in October and November. The English research vessel

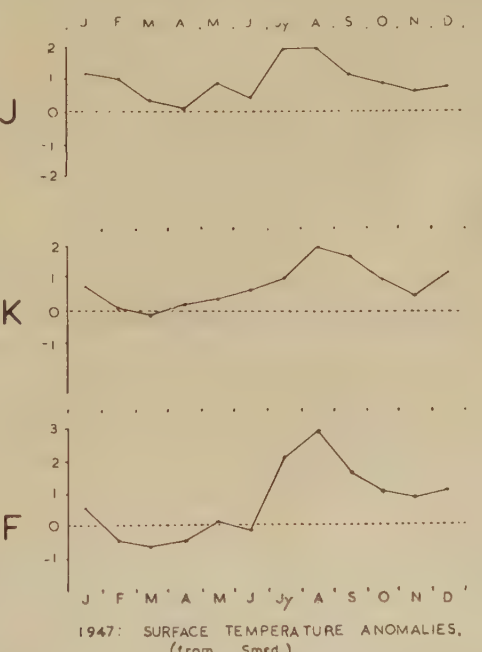

Figure 2. The surface temperature anomalies in 1947 of areas 'J', 'K' and 'F', figures taken from Smed.

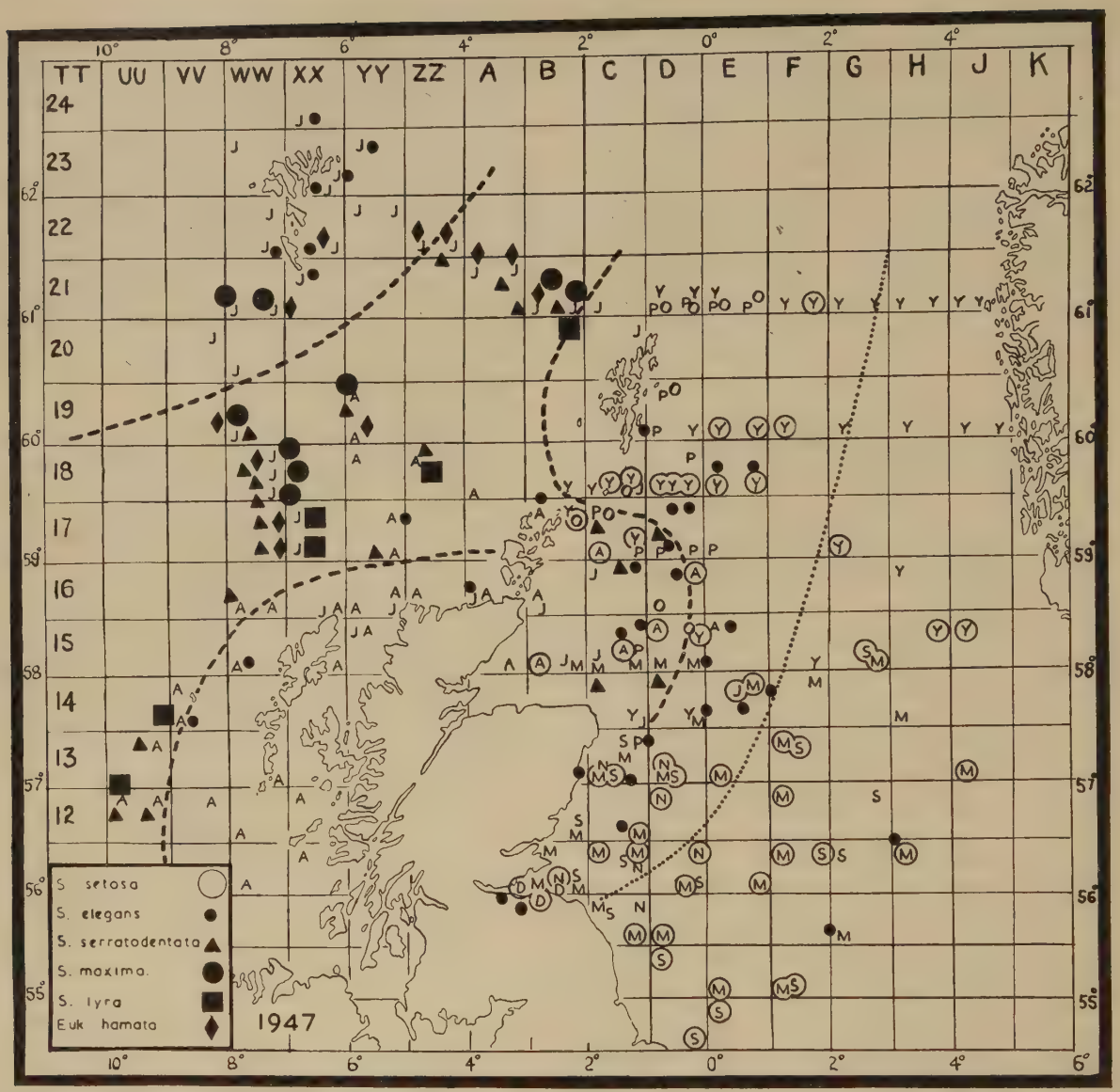
TT UU VV WW XX YY ZZ A B C D E F G H J K
10° 8° 6° 4° 2° 0° 2° 4°
62° 61° 60° 59° 58° 57° 56° 55°
S. setosa
S. elegans
S. serratodentata
S. maxima
S. lyra
Euk. hamata
1947

Figure 3. The distribution of Chaetognatha in 1947. In this chart, and in Figs. 4 and 5, the positions of the plankton stations are shown by a letter indicating the month of the year: P = April, M = May, J = June, Y = July, A = August, S = September, O = October, N = November, D = December. The positions are given only to the nearest sub-square and symbols representing the presence of organisms are placed conveniently near the appropriate station position. The dotted line indicates the hypothetical northerly limit of distributions of *Sagitta setosa* in years of normal Atlantic inflow into the northern North Sea. The distribution of one species—*S. serratodentata*—in spring and summer is outlined by the broken line as an example of how the chart may be read.

"Sir Lancelot" found them in October at the stations indicated on the chart (I am indebted to Mr. J. G. Cattley of the Fisheries Laboratory, Lowestoft, for details of these catches). The evidence from the doliolids is supported by the distribution of the copepod *Rhincalanus* and the medusa *Cosmetira*. The former was found widely distributed in the Faroe channel in June but was absent from the 61° N. line and in the whole area of the North Sea east of Shetland and Fair Isle in July; yet it was present west of Fair Isle and north and east of Orkney in July; in the Moray Firth in August; on the Fladen and north of Aberdeen in September; and off the north English coast in November. *Cosmetira* (Fig. 5), had presumably already passed the entrance to the Faroe Channel when sampling was carried out in June but it was by that time

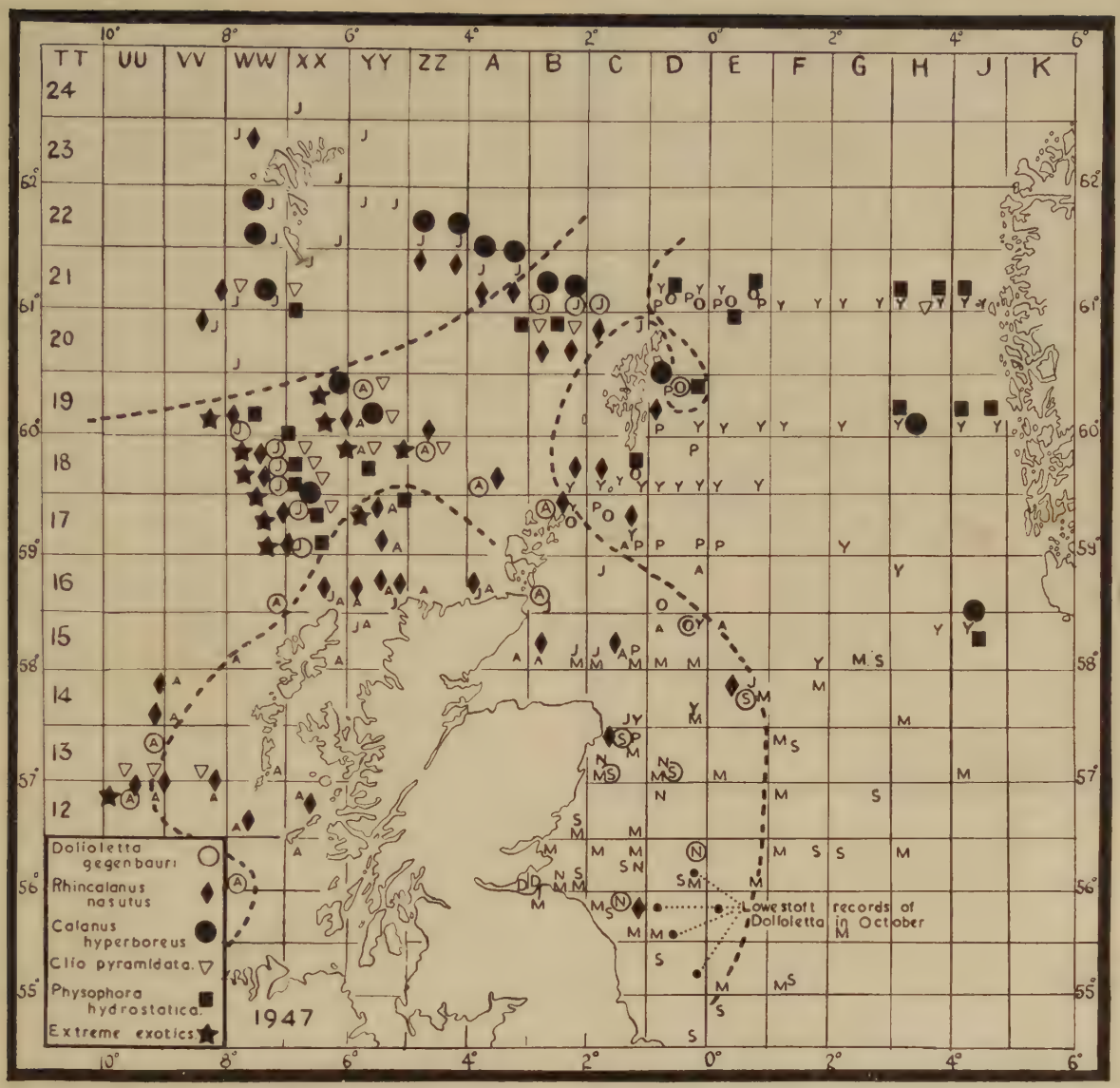

Figure 4. The distribution of some of the indicator species in 1947. (See legend to Figure 3.) The broken line illustrates the limits of distribution of *D. gegenbauri* in summer and autumn, and is included as an example.

found on the Faroe-Shetland line at the south-east end only and close inshore along the north coast of Scotland. It was also found on both sides of the Pentland Firth by which route it had apparently already reached the Moray Firth. In July it was found north-east of Shetland with a few specimens also east of Shetland, and it was found at the western four stations only (where *Obelia* was absent) on the line through the Fair Isle passage but not at the eastern four stations (where *Obelia* was present). *Obelia* is here significant in that its distribution is coastal irrespective of temperature or salinity and so it was found abundantly off all the west, north and east Scottish coasts but was absent in areas where coastal waters are displaced by (not mixed with) oceanic water.

The presence of arctic water is also illustrated by the cold water species *Calanus hyperboreus* (Fig. 4) and the larvae of *Sergestes arcticus* with also the larvae of *Myctophum arcticum* and *M. glaciale*, the distribution of which extended over most of the full length of both the Faroe-Hebrides and Faroe-Shetland lines except for their eastern ends, whilst *Calanus hyperboreus* was also found to the immediate east of Shetland in April.

The hydrography of the Fair Isle passages has long

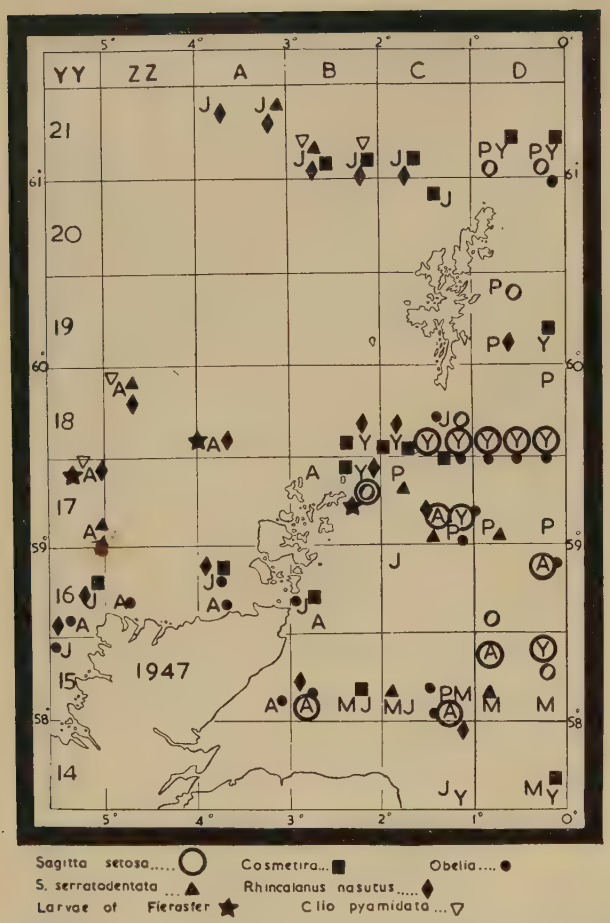

Figure 5. The distribution of indicator species in the neighbourhood of Fair Isle in 1947.

been a question of considerable interest to the hydrographers. Tait (1930, 1931 and 1934) as long ago as 1930 argued that, on the whole and contrary to popular belief, these passages cannot be regarded as a through route for the entry of oceanic water into the North Sea. This theory as applied to the main passage, i. e. between Fair Isle and Shetland, is amply borne out year after year by the plankton indicator species. For instance in 1947 to the west (oceanic side) of Fair Isle we find *Cosmetira* and *Rhincalanus* and on the eastern side *Obelia medusae* and *Sagitta setosa* with only a small area of overlap about Fair Isle (Fig. 5). The two sides of this passage thus had a quite different plankton content and a through current was certainly not occurring at that time. However, to the immediate north of Orkney, we find that there is a route of inflow in 1947, transmitting *Sagitta serratodentata*, larvae of *Fierasfer*, *Cosmetira*, *Rhincalanus* and doliolids (Figs. 4 and 5). It would appear that the oceanic forms entering the North Sea by the Orkney-Fair Isle passages in 1947 were not carried through by a vast influx of water but rather that these few organisms that did go that way were later widely distributed over the north-western North Sea area. The doliolids, which were found in quite large numbers, had probably been stimulated to breed by the warm surface temperatures, so that a few oozoids had produced numbers of small gonozoids which had not themselves been brought in from the Atlantic. Such an increase in oceanic species in the North Sea without a large influx of oceanic water could only occur in forms such as doliolids which are tolerant of somewhat lower salinity conditions but which require a suitable high temperature to thrive. It will be remembered that 1947 was an exceptionally warm summer which, of course, warmed the surface waters only, thus accounting for Smed's surface high positive anomaly in Area 'F'.

There is thus evidence from the distribution of plankton indicator species to suggest that in 1947 there was a tongue of oceanic water penetrating the Faroe Channel along its south side, while the northern side contained an admixture of cold water which prevented the bulk of the oceanic water from reaching the Faroe-Shetland line; and that only a small proportion of the reduced amount reaching Shetland penetrated the North Sea east of Shetland. There was, however, a leakage of water, which though already diluted to rather less than 35 $^{0}/_{00}$ salinity nevertheless contained oceanic elements, into the North Sea by the immediate north of Orkney, and this water became distributed over the whole Scottish east coast area south of 59° where it was mixed with warm surface waters. There was no inflow of water by the passage north of Fair Isle. This picture agrees very well with that produced by the hydrographers, with the additional evidence of the Orkney leakage which would be a small amount of water compared with the North Sea and so easily hidden by dilution, in particular by the rapid rise of temperatures there due to solar radiation. Similar correlations for the years 1920—1939 based on the distribution of salps and doliolids have already been published (Fraser 1949 a) and for the years 1936—1950 based in particular on the distribution of the *Chaetognatha* are now ready for publication.

It must be emphasized that the deductions made from the distribution of plankton indicator species are indications and not assertions, although at times the evidence may be very strong. Nevertheless, because plankton consists of discrete organisms that can be positively identified even from abnormal environments it can be seen that the value of plankton indicators in tracing the actual paths of oceanic currents are several:—

1. They provide a method of tracing the major paths in a given locality, giving on the spot results.
2. They can be used to give pointers where the conventional methods are open to alternative explanations.
3. Under suitable circumstances they can be used to indicate small currents, but possibly important ones

ecologically, when the volume of water may be too small or the differences too slight to reveal significant changes on hydrographical examination, and therefore they can at times, suggest the final areas of dispersal of water which has become too diluted to be recognised by other methods.

Another use that can be made of plankton indicators is the separation of water masses that have, for various reasons, differing plankton content, and therefore differing productive potentialities. Such differences, however, are by no means wholly dependent upon current systems and are therefore beyond the scope of this short paper.

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7.

Water Movements over the Continental Slope in Relation to Fisheries Hydrography.

By

L. H. N. Cooper.

When in 1939 Mr. G. A. Steven and Mr. P. G. Corbin had completed their investigations on the biology of the mackerel in the Celtic Sea, they asked for an assessment of the hydrographical background based on their measurements of temperature and salinity. Since in our area it has never been possible to correlate salinity with much else, no help could be given. But, to attempt an answer, a long-term investigation of the movement of water masses in the area has been started. The archives already contained much data whose full signifiance could not be understood without the use of recent additions to knowledge. It soon became clear that we have to deal with at least four water masses with similar temperatures and salinities but utterly different physical and biological histories. These are:—

(1) The North Atlantic Central water from well out in the Atlantic conforming to a well-defined temperature-salinity relation.

(2) 'Mediterranean' or, better 'Gulf of Gibraltar' water from around 800—1100 m. able on occasion to affect surface conditions.

(3) 'Cascaded' water formed in winter in the shallow waters of the west European continental shelf.

(4) Water formed by 'capsizing' of large water masses over the continental slope during high on-slope winds.

The tentative properties of these waters are set out in Table 1.

Matthews (1914) had established that the dominant circulation in the Celtic Sea (for definition, see Cooper and Vaux, 1949) is cyclonic. Oceanic or Biscayan water enters from the south, passes the entrances of the English and Bristol Channels and escapes south and south-west of Ireland.

In cold winters the shallow seas south of Ireland are cooled and become heavier than the waters in the neighbouring Atlantic down to 250—400 m. depth. This heavy water flows over the edge of the continental slope south-west of Ireland during the late winter and early spring months like a slow but majestic cascade. Cooper and Vaux (1949) have shown that in 1927 the water feeding this cascade flowed westward at about 0.6 miles per day.

Observations, taken by the Irish Fisheries Service at stations S and T in May 1913 (Figs. 1 and 2), were intelligible only if such cascade water had become concentrated within a submarine canyon cutting back like a gutter into the continental shelf. Attention is drawn to the shape of the T—S curves below 128 m. at station S and below 274 m. at station T which are considered to represent essentially the same mass cascading down a submarine canyon. No such canyon was known although other somewhat insecure observations suggested its existence. Through the cordial co-operation of the Hydrographer of the British Navy, Rear-Admiral A. Day, C.B.E., D.S.O., H.M. surveying ship "Cook", under the command of Capt.

Table 1. Some Predicted Properties of the Several Types of Water Mass found near the Continental Slope of the Celtic Sea.

	Oxygen %	Silicate – Si μ g.-atom/l.	Total Phosphorus μ g.-atom/l.	Temperature ° C.	Salinity ‰
Cascaded Water	> 85	< 4	< 0.7	Uniform and dependent on origin	
Capsized Water	High and uniform	ca. 6	ca. 0.9	Uniform and > 10	Uniform and > 35.5
Gulf of Gibraltar Water	65—69	10—11.5	1.2—1.3	9.0 ± 0.5	Maximal and > 35.5
Deeper North Atlantic Central Water	65—70	> 10	> 1.3	Conforming to standard T—S diagram	

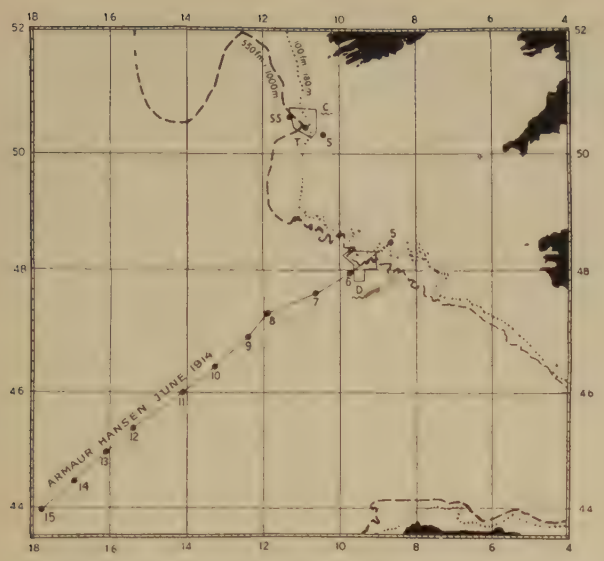

Figure 1. Approximate 100 and 550 fm. contours of the continental slope of the Celtic Sea. These over much of the area are not well established. Area C of preliminary survey by H.M.S. "Cook". Area D of detailed survey by H.M.S. "Dalrymple". Area between 9° and 11° W., surveyed by the French research vessel "Président Théodore Tissier". Remainder assessed from Admiralty charts and Le Danois (1948, Figs. 2–8). More detailed surveys are likely to extend the known areas of highly dissected continental slope. Positions of Irish stations S, T and SS. Here the extent of the indentations as shown may be exaggerated. Line of section (stations 5—15) worked by "Armauer Hansen" in June 1914.

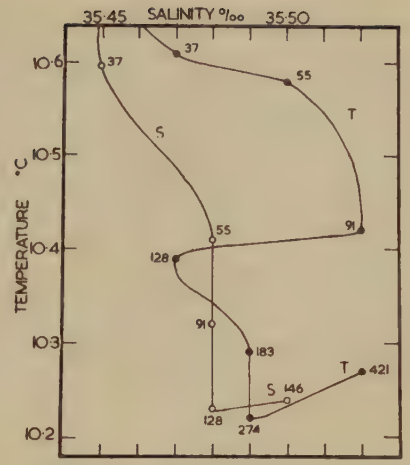

Figure 2. Temperature-salinity diagram for two stations worked by the Irish research vessel "Helga" on 15. May 1913. Station S, 50° 18′ N., 10° 22′ W., depth 154 m. Station T, 50° 26′ N., 10° 51′ W., depth 444 m. The figures against the curves give depths of observations in metres.

Kenneth Collins, R.N., sought and found this canyon at the predicted position, 50° 30′ N., 11° 00′ W. although bad weather prevented more than a skeleton survey within the area C on Fig. 1. Since accurate contouring is not yet possible, the shape of the indentation as shown is schematic only. The success of this prediction gives reason for believing that submarine canyons do indeed canalize cascade currents.

It strengthens our suspicion that some very odd results reported by Helland-Hansen and Nansen (1927) and Gaarder (1927) on "Armauer Hansen" in June 1914 are to be explained by a core of highly oxygenated cascade water canalized in such a submarine canyon and projected 200 miles from the slope into the ocean (Table 2). The fact that the oxygen-rich layer lay deeper at the outer station 11 agrees with a thesis propounded by Sandström and confirmed by other work at Plymouth that such currents move forward with a right-handed corkscrew motion.

Acceptance of these ideas would be easier if we could make direct current measurements in and around the submarine canyon at 50° 30′ N., 11° 00′ W. in March and April following a cold winter.

Animals and plants unable to swim out of the cascading water will be carried on and down. Plankton animals able to swim, especially those which undertake diurnal vertical migrations towards the surface, would swim up from the cascade into the relatively stationary overlying apron of warmer more oceanic surface water. Vertical migration should therefore tend to concentrate the more vigorous zooplanktonts from the cascade into a zone, often narrow and stationary, in the more oceanic surface apron. Such con-

Table 2. Core of Celtic Sea Cascade Water observed by "Armauer Hansen" on June 7, 1914.

Depth m.	Oxygen cc./l.	Oxygen %	Salinity ‰	Temperature ° C.	Density σt	Nature of Water
Station 11, 46° 00′ N.			14° 03′ W.			
400	5·45	85·5	35·45	10·25	27·28	North Atlantic Central
600	4·83	76	35·38	10·24	27·22	?
800	*5·48*	*86*	*35·43*	*10·17*	*27·28*	*Celtic Cascade Core*
1000	4·55	68	35·50	7·95	27·69	Mixed Gulf of Gibraltar and N. Atlantic Deep
Station 10, 46° 25′ N.			13° 14′ W.			
400	5·44	86·5	35·52	10·82	27·23	North Atlantic Central
600	*6·01*	*94·5*	*35·45*	*10·36*	*27·26*	*Celtic Cascade Core*
800	4·07	64·5	35·73	10·44	27·48	Gulf of Gibraltar
1000	4·38	67·5	35·68	9·25	27·63	Gulf of Gibraltar

centrations are likely to be sought by pelagic fish. This picture should apply where the cascade flows over a smooth slope. If, however, the slope should be dissected by strongly developed submarine canyons, heavy cooled shelf water should collect in these so that an even more strongly differentiated distribution should come about in the surface apron immediately above. In cold winters the most productive regions of all may lie above submarine canyons in the continental slope.

The economic conclusion is that in the apron of more oceanic water overlying a cascade, pelagic fish are likely to find concentrations of food greater than anything to be found on the continental shelf. Pelagic fish are also likely to find good feeding in 'cascade cores', such as that apparently observed by "Armauer Hansen" in June 1914.

Over banks in shallow water a comparable small scale phenomenon is likely in autumn. Steven (1951) has found that these several cascading hypotheses provide a satisfactory explanation of the habits of mackerel in the English Channel and Celtic Sea. There mackerel become demersal and congregate on declivities at times when cascading would be anticipated.

The behaviour of herring in the Norwegian Deep, as described by Balls (1951, especially pp. 288—89) is in line with this prediction. In Norwegian waters a purse seiner may catch in one haul as much as an average drifter catches in a year. However, between the entrances to Oslo and Sogne Fjords the Norwegian continental shelf is far too narrow for cold water to be formed locally in sufficient quantity to cascade. Again, this shelf is often invaded in winter by large quantities of Baltic water which, although cold, is of low salinity and too light to cascade.

In strong contrast the North Sea Plateau around the Viking Bank to the west of the Norwegian Deep is well suited for producing cascade water in large amounts. Thus on 27. March 1939 the Scottish research vessel "Explorer" (Cons. Internat., 1944) found at four stations lying in 108—140 metres depth: 60° 01′ N., 01° 12′ E.; 60° 20′ N., 01° 46′ E.; 60° 41′ N., 02° 08′ E. and 61° 01′ N., 2° 00′ E., an area of almost homogeneous water with density exceeding σ_t 27.65. This water, possibly a cascade feeder current, was heavier than anything observed that winter by "Armauer Hansen" and "Johann Hjort" in the Norwegian Deep, even at depths greater than 300 m. Considerable cascading may have occurred. On this view, in many years much of the bottom water of the Norwegian Deep may not have come directly from the Atlantic Ocean but may have spent a winter over the Northern North Sea Plateau.

Runnström (1941, p. 40) described a herring shoal about 7. February 1937 between the Viking Bank and Holmengrå outside the Sognesjø. It was at least 20 nautical miles long, 2 nautical miles wide and about 30 m. thick. A shoal shaped like this suggests a cascade core laden with food from the Plateau and canalized by a submarine canyon in the neighbourhood of the Viking Bank. Herring are likely to concentrate in such a core through which they, and some of their food organisms, may make diurnal vertical migrations.

The stocks of herring exploited by the Norwegians appear to be composite. Whereas spawning herring on the narrow Norwegian banks are not likely to be much affected by cascading, locally non-existent, the distribution of herring and mackerel in the Norwegian Deep and along its western declivity may well be controlled in late winter by cascading from the Northern North Sea Plateau. Moreover, cascading into a parallel-sided channel requires that compensation water must escape somewhere else, either as a deep current into the Atlantic or by enforced upwelling along the Norwegian coast. Such a mechanism would contribute to the well known productivity there but would vary greatly in strength from year to year.

Abreast of the Celtic Sea, the physical oceanography suggests that there may be no considerable submarine canyons north of the one discovered by H. M. S. "Cook" at 50° 30′ N., 11° 00′ W. Here there appears to be another quite different way in which heavy cooled water leaves the shelf, that is, by a water mass being pushed off over the edge with considerable momentum imparted by the water pressing behind. Just as a heavy cricket ball may be thrown into the air and remain aloft so long as it has momentum, so this water mass may persist awhile suspended over somewhat lighter water. A density inversion may result. By means of the density inversion the subsequent history of the projected water mass may be followed until its identity is lost by mixing with the water below. It turns to the right and then traverses the side of the continental slope in the way that a well engineered mountain road may traverse the side of one of the mountains bordering a pass. During its traverse such a current may fall with a gradient of about 1 : 1000 and move forward with a horizontal right-handed screw motion. No suitable descriptive name for this process has yet been found.

The part, possibly important, played by submarine canyons in controlling water exchanges over the continental slope recurs frequently in this narrative. It is a matter of note that soundings by the French research vessel "Président Théodore Tissier" (Beaugé, 1934) and by H. M. surveying ship "Dalrymple" (Cooper, 1952 b) have shown that the continental slope west of the English Channel is far more dissected

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Holtedahl's (1940) bathymetric map of the Norwegian Channel has since been examined. In the west wall no such submarine canyon is shown. The west wall runs north and south and over it lines of soundings run east to west and about 5 miles apart. A submarine canyon between these lines could easily have escaped observation. A north-south line of echo soundings between 60° 20′ and 60° 50′ N. along the 200 m. contour as shown on Holtedahl's map would quickly show whether this possible explanation of Runnström's observation has any basis in fact.

than was once thought. The possible control exercised over cascading water by submarine canyons, such as that at 50° 30′ N., 11° 00′ W., has already been mentioned while 'cascade cores' could, it would seem, arise nowhere else.

The hypotheses of cascading deal only with a way in which water, whether it be rich in nutrients or poor, leaves the continental shelf over the continental slope. No adequate mechanism has been recognized for explaining the great variation in nutrient resources and of potential productivity of the waters which enter the English Channel from the south-west. The classical theorem of upwelling due to off-shore or 'off-slope' winds does not seem adequate by itself to account for what has happened. A process which appears powerful enough to explain what has happened can now be envisaged but has not yet been proved conclusively. It has however fitted with all the relevant observations which have been so far examined.

All the evidence suggests that new water, bearing properties which spell success or failure for the fisheries, enters the Celtic Sea and English Channel over the continental slope between Ushant at the north-west corner of France and the Sole submarine promontory 250 miles to the west. No evidence has ever been found that the Atlantic surface waters are ever rich enough to account for the enrichment of the English Channel in the nineteen twenties. Although the existence then of sufficiently rich oceanic water cannot be excluded, it is much more probable that the enrichment was brought about by some form of upwelling. I suspect that the cause was composite and that several distinct mechanisms combined together to produce an exceptional degree of upwelling. Each possible component mechanism needs separate study.

There may be two distinct effects of a strong wind blowing on to the continental slope from the south. Such a wind will first force light nutrient-poor water against the slope to form a cushion of considerable depth above sloping surfaces of equal density—stable only while the wind lasts (developed from Sandström, 1918). Potential energy has become stored in the water. As soon as the wind has died down and the stress has been removed from the sea surface, the potential energy becomes converted to kinetic energy. The surfaces of equal density then oscillate about their mean level. The conditions against a continental slope are rather different from those in a tank with vertical walls. When the heavy deeper water rises against the slope, it would spill over the edge on to the continental shelf. Some mixing and enrichment with nutrients of continental shelf water would occur but the effect is unlikely to be great and important only locally.

But in a submarine canyon, which becomes narrower and shallower as it cuts back into the shelf, such spillage water would become canalized into a spurt of water. Conditions would come to resemble those which create at the surface a tidal bore or eagre in the rivers Severn and Trent. It would seem that such a constricted bore or eagre of deep water could be projected many miles on to the continental shelf whence it would return only slowly on the next downward swing of the boundary layer over deep water. This mechanism would be especially favoured if a submarine canyon in the slope heads into one of the shallow troughs which dissect the southwestern Celtic Sea. Indeed it would provide a means for preventing such troughs from silting up.

The inference is that areas of the sea lying immediately shorewards of a submarine canyon should be especially favourable for outbursts of phytoplankton not only in spring but in summer as well. Submarine eagres of this kind may well occur often but seem insufficient to account for much enrichment of large areas such as the Celtic Sea.

It appears likely that the occasional shoals of boar fish, *Capros aper*, found in the English Channel have been introduced on to the continental shelf by such submarine eagres which have detached the fish from their permanent home amongst the corals of the continental slope and submarine canyons. If this is so *C. aper* would provide a valuable biological indicator of water movements from certain well defined areas.

Sandström (1918) further developed his idea into his concept of 'jibing' of water masses in a high wind, a process which seems especially likely to happen along the continental slope of an extensive continental shelf such as that of the Celtic Sea, of the Porcupine Bank area and of the Northern North Sea Plateau or along the insular slope of the Rockall Table Mount. This hypothetical process, fully described elsewhere (Cooper, 1952 a), is not readily summarized. It is visualized that a gale of wind blowing from the ocean against a continental slope will first create a sandwich of heavy water between layers of lighter water. This unstable sandwich may then 'capsize' leading to very thorough vertical mixing to a depth of several hundred metres. Within this highly homogeneous water mass there is no restriction on intense vertical and horizontal circulation. The depth of capsizing increases as the gale proceeds and a sharp discontinuity develops at the base of the water mass. Across this discontinuity deeper water, richer in nutrients, is continually being drawn while the gale lasts. Such enriched capsized water may then be blown on to the continental shelf which it will enrich. Moreover the nutrient content of the water passing on to the shelf should increase as the gale proceeds and the depth of capsizing becomes greater. To accord with Ekman's theory the gales from the ocean most favourable for capsizing will blow not at right angles to the continental slope but at an acute angle with the continental slope on the right. The name 'capsizing' seems preferable to 'jibing'.

South-west of Ireland the continental slope forms one wall of a considerable submarine indentation hollowed out of the Porcupine Bank. Here the gales most favourable for capsizing will blow from south-west and west, the direction of the prevailing and

strongest winds in the area. Such gales are commonest in winter and may then combine with cascading and resonance phenomena in the submarine indentation to produce vertical mixing to a very considerable depth as illustrated in Figure 3 (Stations SR 2158 and 2244 = station SS of Figure 1). The waters here most concerned will be either oceanic surface water or water recently cascaded from the continental shelf. In this area, in spite of the presumed occurrence of much capsizing there may only rarely be much enrichment of the shelf with fresh nutrients on any considerable scale. Even when enrichment occurs there, the Porcupine Bank is more likely than the Celtic Sea to benefit owing to the cyclonic circulation. Whenever cascading plays a part it will tend to reduce enrichment from deep water by any other mechanism.

Along the southern edge of the Celtic Sea, winds most favourable for capsizing will blow from the south-east or south. These winds are less common than the south-westerlies and westerlies. Moreover in this area there is likely to be much less cascade water, often none at all, so that, if capsizing occurs, it may bring about mixing with the deeper North Atlantic Central water or even with Gulf of Gibraltar water at 800—1200 m. depth, both relatively rich in nutrients. All in all, the most favourable conditions for enrichment of the southernmost Celtic Sea by capsizing are likely to occur after the breakdown of the summer thermocline in autumn. Southerly gales in November and December are likely to be more effective in bringing up nutrients than those in February and March. The usual cyclonic circulation of the Celtic Sea will tend to transport such enriched water on to the continental shelf and into the English Channel.

Capsizing is envisaged as essentially a wave phenomenon and may be compared with the breaking of a roller approaching a beach. By analogy with what happens to a swell approaching an ordinary coastal bay, over a submarine terrain such as that of the continental slope of the southern Celtic Sea there should be a tendency for the destructive energy created by capsizing to be concentrated over the submarine spurs and for the headings of the valleys to be relatively quiet. Capsizing as a mechanism for surface enrichment with nutrients is likely to be more effective over strongly dissected sections of the continental slope than over smooth areas.

It seems probable that winds of a given strength will be very much more effective in producing capsizing if preceding conditions have been optimal. Many variations of circumstances may be visualized. Thus, if strong winds have blown from between north and east, as they did in February 1947, some degree of upwelling by the classical mechanism would occur. If then the wind went quickly to the south, reaching gale force and producing severe capsizing while nutrient-rich water stood banked high against the slope, there would arise very favourable conditions for surface enrichment of a kind which would occur only a few times in a century.

In a submarine indentation such as that in the southern part of the Porcupine Bank internal waves probably resonate strongly, causing great turbulence and vertical mixing and, by so doing, destroying themselves. In this indentation combined studies of cascading, capsizing, internal waves and resonance will be necessary. Capsizing against either wall of the indentation should itself induce deep internal waves which would be expected to resonate strongly. Similar resonance is to be expected in the Norwegian deep when the waters are stratified although the necessary initial capsizing may be largely confined to the western wall with easterly or north-easterly winds.

There is one more theoretical issue. The exceptionally powerful vertical thrusts, visualized as occurring beneath a capsizing water mass, must be followed by subsidence of the relatively heavy new surface water and recovery of the deeper water of the same density into a thinner but more extensive lenticular water mass at mid-depths. This is a process which must necessarily initiate wave motion in the lower boundary of the homogeneous layer. It provides a possible mechanism for creating the deeper internal waves observed in the ocean.

A stratified or laminated water mass underlying a

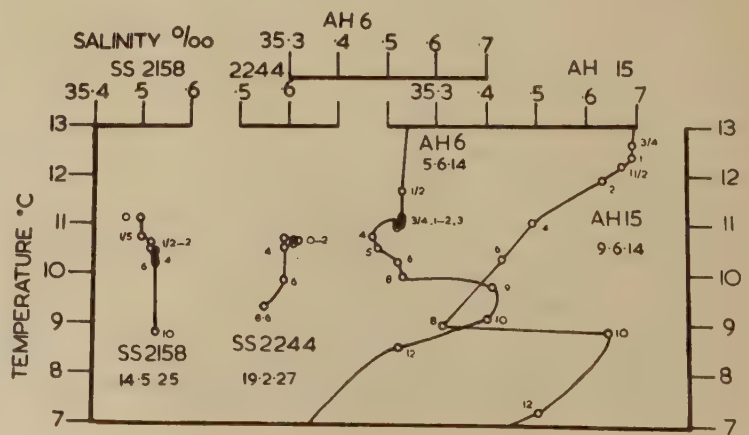

Figure 3. Temperature-salinity diagrams with depths of sampling indicated in hundreds of metres; (a) at "Armauer Hansen" station 1914/15, a typically oceanic station with North Atlantic Central water at 100—800 m. and Gulf of Gibraltar water at 1000 m.; (b) at "Armauer Hansen" station 1914/6 near to the highly dissected continental slope of the Celtic Sea. North Atlantic Central water was absent. This curve and the remaining two at the Irish station SS on 14. May 1925 and also on 19. February 1927, when cascading is believed to have been proceeding strongly, show the compression of properties which may occur near to a continental slope. Vertical mixing may be intense to 400 m. and effective even to 1000 m. depth.

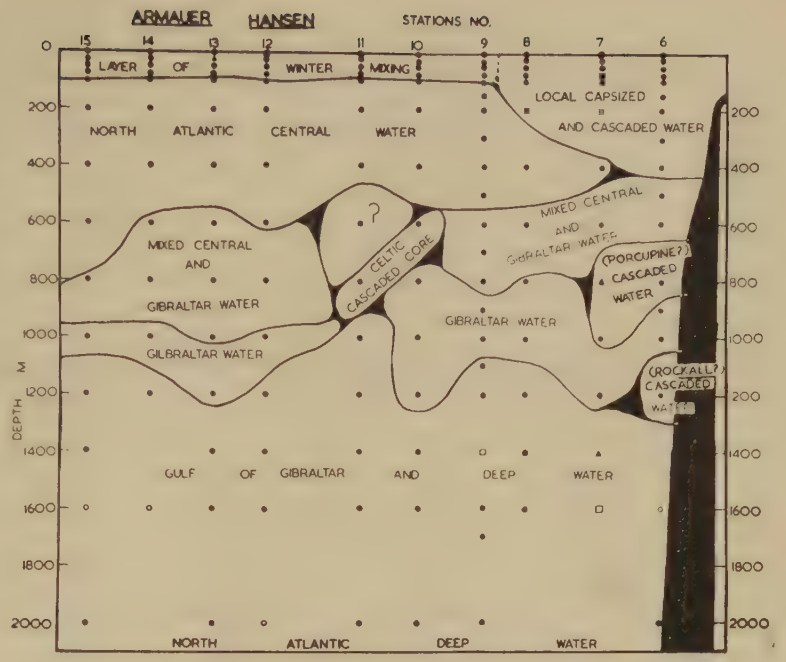

Figure 4. Vertical section illustrating distribution and possible origins of water masses at "Armauer Hansen" stations 15.—6. June 1914. Circles represent determinations of temperature and salinity, squares represent determinations of temperature only, and triangles of salinity only. Where oxygen determinations were also made these symbols are blacked in. Helland-Hansen and Nansen's interpolated results at intermediate depths have been used in constructing the section.

quiescent one, already homogenized by capsizing, may be compared with the leaf spring of a railway wagon or motor car at rest. In the open ocean, the vertical thrust due to subsequent capsizing—if indeed such ever occurs there—would be taken up by the laminated water mass as by a leaf spring and the energy smoothly dissipated as internal waves. There is no reason to believe that much dissipation of energy would occur due to friction or turbulence. But against a continental slope and especially against a strongly dissected one this 'leaf spring' of laminated water masses would grind forcibly so that much of the energy of the vertical thrust would be dissipated by turbulent mixing. Detailed examination of the Irish records at station SS has shown that such mixing occurs there between 600 and 1000 m. Two of the most extreme occurrences have been presented in Figure 3.

'Leaf spring' dissipation of energy beneath a capsizing water mass against a dissected continental slope may provide a mechanism able to transmit to very considerable depths energy imparted to the surface of the sea by the wind and of sufficient magnitude to produce the observed distribution of properties between 600 and 1000 m.

Using the ideas here presented, it has been possible to construct a vertical section of the distribution of water masses on the basis of the "Armauer Hansen" observations in June 1914 (Figs. 1 and 4). The highly oxygenated water at 800 and 1200 m., too cold to have been formed in the Celtic Sea has been tentatively attributed to the Porcupine and Rockall Banks. The evidence for Rockall cascade water in this area is fully discussed elsewhere (Cooper, 1952 b).

Fraser (1950) has stated that the Scottish fisheries research vessels have found biological indications of two water masses approaching Faroe from the southwest. One, the 'Lusitanian' stream, has travelled via the west coasts of Ireland and Scotland and will have been influenced by vertical exchanges over and along the continental slope; the other, the 'Atlantic' stream, travels farther west. The two streams, at least in the middle and late summer, are said to be very distinct although mixing along the line of meeting. May one ask whether the 'Lusitanian' water may be identifiable with 'a capsized and cascaded water' similar to that at stations 6—8 of Figure 4. Such water should exist all along the continental slope west of the British Isles and for 75—150 miles to seaward. The 'Atlantic' water of the Scottish workers would then be identifiable with the 'North Atlantic Central' water of stations 9—15 of Figure 4 and its winter-mixed surface skin.

The North Atlantic Drift carries warm-water plankton organisms ever northwards and eastwards into colder regions unsuitable for their reproduction. Any mechanism for returning part of the stock to the south should assist its survival. If therefore there are any organisms, not only animals but perhaps diatoms as resting spores, which can avail themselves of the return current of Rockall cascade origin, their survival should be favoured. Diatom resting spores could only profit if they complete their travels by being brought up to illuminated surface waters by some form of upwelling such as capsizing.

This paper presents a group of interlocking hypotheses, very far from being proven but consistent with such observations as have been examined. They require further examination in the mathematical and biological laboratories and at sea.

Summary.

Processes of exchange of water over the continental slope between the ocean and the continental shelf have been discussed. These are: (a and b) two distinct processes of cascading of heavy water over the slope due to cooling of shallow seas in winter, (c) in winter, formation of cascade cores projected at depth from submarine canyons into the ocean, (d) formation of submarine 'eagres' or spurts of water projected up submarine canyons on to continental shelves after strong on-slope winds have died down, (e) 'capsizing' of large water masses over the continental slope during high on-slope winds, and (f) turbulent dissipation of energy in deep stratified water lying against a continental slope as the consequence of 'capsizing' of overlying water.

The nature of the water masses recognized along a section worked from the Celtic Sea into the Atlantic in June 1914 by "Armauer Hansen" is illustrated in Figure 4.

Some biological consequences of the theories are also developed, viz. (a) in some winters, an apron of surface overlying the continental slope should become rich in those zooplanktonts which migrate vertically, (b) an explanation of the seasonal concentration of mackerel over declivities of the sea bed, (c) a possible explanation of an elongated herring shoal in the Norwegian Deep as due to concentration of food and fish in a cascade core, (d) a mechanism by which cascading from the neighbourhood of the Viking Bank might in some winters cause enforced upwelling of nutrient-rich compensation water along the Norwegian coast, (e) the boar fish may be introduced into the English Channel by submarine eagres, (f) the distinctive 'Lusitanian' and 'Atlantic' waters recognized biologically by Scottish workers near Faroe are tentatively identified with 'capsized and cascaded' water and North Atlantic Central water.

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8.

The Influence of Hydrographical Factors on Fish Stocks and Fisheries in the Transition Area, especially on their Fluctuations from Year to Year.

By

Aage J. C. Jensen.

Of all the north and west European seas—and indeed of all seas in the world—the Transition Area is for the present best suited for studies of the influence of hydrographical factors on the fish stocks and fisheries. This is so for two groups of reasons:—

I. The natural conditions.

1. The great differences in salinity between the ocean water in the Skagerak and the brackish water in the Baltic.

2. The great difference between the summer and winter temperatures.

3. The short-time fluctuations of salinity due especially to the irregular changes of the currents.

4. The large fluctuations from year to year of the monthly means of salinity and temperature.

Natural conditions which are just as good, or in some cases even better, are to be found in some other seas, but they would be of but small value if their fluctuations were not regularly determined.

II. The continual registration of facts.

1. The regular observations of currents at the surface, and salinity and temperature at various depths, taken each day from many light-vessels and coastal stations distributed over the area and supplemented at regular and irregular intervals by observations from the hydrographical and biological laboratories.

2. The quantitative and qualitative control of the stocks of some of the most valuable commercial fishes, from the eggs and larval stages to the adult fish, carried out each year from the fisheries laboratories during a long series of years.

These were started in 1905 from "Kommissionen for Havundersøgelser" (by A. C. Johansen) with the yearly investigations of the quantity of the 0- and I-group plaice at the coasts. Since 1923 the stocks of older fishes were investigated regularly each year from the Danish Biological Station. Also from the Swedish Hydrographical-Biological Commission, from the German Commission, from the Flødevigen Hatchery and other institutions such yearly investigations of the fish stocks have been carried out. These yearly records of the quantitative and qualitative composition of the stocks were preceded by records taken at more or less regular intervals since the beginning of the century, or in some cases since the '90's.

Mention must also be made of the quantitative and qualitative investigations of the invertebrate bottom fauna undertaken by C. G. Joh. Petersen since the beginning of the century.

3. The fairly precise fishery statistics collected by the ministries.

Naturally such material admits of wants and omissions which seriously hamper the investigations of the hydrographical influences on the stocks: e. g., regular observations of the currents at deeper levels at some few selected places would prove of very great value, and the fishery statistics would be of much more value if "catch per fishing unit" could be given in more cases than now. The Swedish fishery statistics include information on some fisheries which enables a calculation of catch per cutter or per implement in each season.

On the basis of the material mentioned a great many investigations have been carried out. This paper gives a short summary of the results with some critical appraisals. This summary lays no claim to completeness. It certainly might have been more detailed and no doubt more results and statements might have been given, but often it is very difficult to guess the real value of statements which are largely hypothetical. It is very easy to put forward hypotheses, when there is not sufficient material for checking the various possibilities, and a great many have been put forward. I have omitted some of the idle hypotheses, and I think it is almost certain that I have omitted some which in the course of time will prove valuable.

A. The Influences on Eggs and Larvae.

1. The Survival.

The strength of the year-classes of **plaice** was found by A. C. Johansen in 1908 (30) to be positively correlated with the surface salinity, and he thought that this was because the eggs at low salinities would sink to the bottom (cp. 12) where many of them must perish. He also mentioned that extraordinarily low temperatures possibly help to produce unfavourable years for the development of the young, being injurious to the plaice at the spawning time, or in its earliest stages of development (30, p. 44).

Next, H. Blegvad (1 and 2) demonstrated a positive covariation with the winter temperature and explained it as a direct effect mainly due to the prolongation of development caused by low temperature. A subsequent examination by A. C. Johansen (36) confirmed the positive correlation with the surface salinity. He now came to the conclusion that in cold winters, when there is a relatively marked outflow of comparatively fresh water, the tiny plaice larvae fail to obtain sufficient nourishment, and die of starvation en masse (36, p. 16) because there is, on an average, less plankton per sq.metre of surface in the Baltic than in the southern Kattegat and the Belt Sea (cp. 53). He found a close agreement between the strength of the year-classes and the plankton volumes in 1903—08 assertained by C. H. Ostenfeld and P. Jespersen.

I described, in a paper in 1933 (18), a negative correlation with the salinity at the bottom. To the previous theories I added a new one: that transport of the eggs through the Belt Sea towards the Baltic destroyed many of the eggs.

Table 1 a and b shows the correlations of the logarithms of the mean number of 0-group plaice in the years 1905—35 with surface temperature and with salinity, respectively. The logarithms are used since their distributions are about normal whereas those of the original figures are skew.

The correlations with the salinity may be due exclusively to the fact that the surface temperature is positively correlated with the surface salinity in the same month (20, p. 17) and that the surface salinity (and surface temperature) are negatively correlated with the bottom salinity ca. 1 month later (20, p. 14).

From the size of the coefficients it may seem that the temperature is the most important factor.

In one of the papers mentioned above (1) Blegvad found also a distinct correlation between the strength of the year-classes of **cod** (deduced from analyses of catches from the Danish Biological Station 1923—26) and the winter temperature, which he attributed to the lethal effect of the cold on the eggs and larvae either directly or through the prolongation of the time for the development causing an increased mortality.

This connection was also subsequently investigated. I found a positive correlation between the yield of the cod fishery in 1912—27 in the Kattegat and the Belt Sea and the temperature during each month from April to July (r: 0.67, 0.63, 0.66 and 0.57 respectively) which was thought to be explained in the same way as by Blegvad (16). The yield of the fishery had increased during these years parallel to an increase in the temperature (Fig. 3 in 16).

E. M. Poulsen (60) demonstrated positive correlations between the mean temperatures in each of the months March, April and May and the mean number

Table 1. Correlation Coefficients (×100) between Logarithms of 0-Gr. Plaice and a) Surface Temperature and b) Salinity (18-20 years in the period 1905-35).

a)

Coast:	Skaw—Hals		Aalborg Bay		W. coast Djursld.	The Sound	N. Belt Sea	S. Great Belt	W. Baltic Lt. Belt
	Temperature at:								
Date/Position:	Læsø	Rende	L. V.		Sch. Gr.	Drogden	Schultz's Gr.	L. V.	Middelfart
December	—11		—12		4	17	15	— 6	— 3
January	23		44		45	45	48	4	32
February	21		49		67	24	65	9	41
March	0		72		37	29	8	—13	14
April	22		67		34	27	15	—22	15
May	26		54		40	12	13	—20	17
June	6		23		22	22	13	— 1	2

b)

	Salinity at:												
Date/Position:	Læsø		Rende		L.V.		Sch. Gr.		Drog-den	Lappe-grund	Schultz's Gr.		L.V.		Middelfart
Depth m.:	0	20	0	26	0	26	0	20	0	26	0	26	0
December	—68	16	—29	36	—19	10	—11	1	16	22	—36	8	—29
January	13	32	25	32	12	14	—17	48	50	— 5	2	11	2
February	42	— 3	34	6	47	—15	41	—50	50	—56	—30	—7	48
March	20	22	41	—11	—18	—40	14	—14	—54	—53	1	—36	12
April	22	6	— 6	—31	—15	—26	26	—14	—27	— 8	—19	—25	—19

of larvae caught during quantitative fishing in the Kattegat and the Belt Sea with the ring-trawl during the period 1923—29. He stated that there was reason to suppose that the connection was due to a large amount of plankton produced by high temperatures. He found also some measure of agreement between the temperatures of the surface water in January and February and the mean number of larvae caught which he concluded must be explained in a similar way.

He later continued the examination (66), and found a positive correlation between the average lengths of the larvae and the temperature in the spring. He found indications of an indirect effect of the temperature through its influence on the plankton production, but he considered that the direct effect of the temperature was probably part of the explanation.

The numbers of herring larvae found in the southern Kattegat and the Belt Sea in September-October show negative correlation with the temperature of the water during the previous July-August.

It has been found (29) that significant negative correlations exist between the numbers of larvae in the regions east of Djursland, around Samsø, the Great Belt and the Sound in October (1927—38) and the surface temperature of the water in June, July and August, respectively (coefficients of —0.4 — —0.6). Moreover, rather high positive correlations exist between the numbers of larvae and the surface salinity in June and July (0.4—0.8), and the bottom temperature in July, August, September (0.2—0.6), and negative correlations of about the same size between the numbers of larvae and the bottom salinity in July, August, and September. The explanation of the connection which I have given in the paper (that the spawning is delayed when the temperature of the upper water layer is higher than normal) cannot be correct, since naturally, in this case there should also be negative correlations between the lengths of the larvae and the surface temperature, and actually there are, for the Great Belt, positive correlations. More likely the cause is that a high temperature in the lower water layer promotes the maturing of the herrings which keep mostly to the deeper water.

For the survival of the autumn herring larvae of the Belt Sea, the Sound, and at Bornholm in the Baltic, the winter temperature seems to be of great importance. The larvae do not develop scales until the next spring, and when the winter is especially cold proportionately more of the tiny larvae will die. We do not have, as yet, sufficient age statistics to determine the strength of the year-classes for more than a few years, but we can compare the yield of the fisheries which are based on the autumn spawners with the winter temperature some years before. The autumn herring fishery in the Belt Sea and the fisheries in the Sound, along the Baltic coasts of Seeland, Møen and Falster and at Bornholm, have been based almost exclusively on the autumn spawners, but in recent years when these herring have been very scarce, the autumn fisheries have yielded mainly spring spawning herring.

From age-determinations of the commercial catches we know that the majority of the herring enter the fisheries when they are three years old. By comparing the yield of these fisheries with the winter temperature 3 years before, we find a rather pronounced correlation (see Fig. 1). Yet it must be remembered that a rich year-class of herring may give rise to a large herring stock and a large fishery for some years until it has been reduced by the fishery and by natural mortality. Therefore a cold winter which comes just after a specially good survival year will not always give a low yield. Thus the diminishing effect on the yield of the cold winter of 1916/17 was veiled by the yield due to the good survival year 1913. From the age determinations of A. C. Johansen (37) we know that this year-class was the basis of a very great herring fishery in the Sound during 1916—20.

In the northern Kattegat the Kobbergrund herring spawning at 20—30 m. depth about October have been the main object of a Swedish drift-net fishery carried out especially in September, October and November from Anholt to Vinga. In some years this fishery has been carried out also off Hallö and Skagen.

The figures below represent the correlation coefficients (× 100) between the Swedish catch of her-

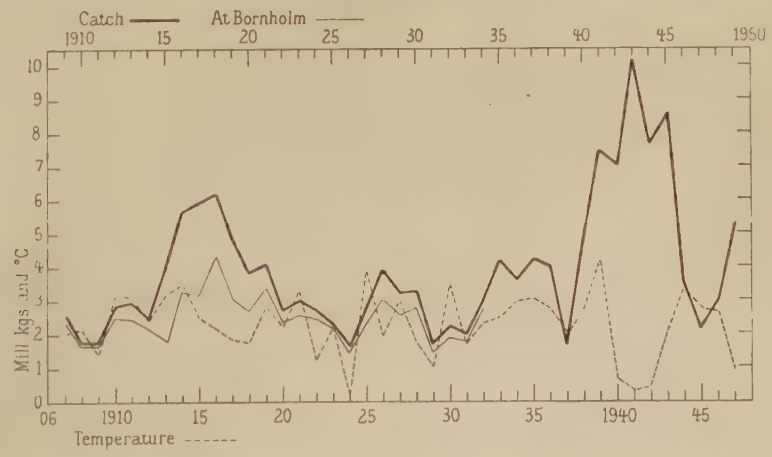

Figure 1. Danish catch of herring in the southern part of the Sound and eastern Baltic (thick) and at Bornholm (thin) compared with the temperature in January, February, March at Christiansø (broken curve).

ring per drift-net and the salinity at Læsø Trindel L. V. and show that in the years 1919—39 a positive correlation existed between the fishery yield and the salinity in the lower layer during August—September 3—4 years before.

Depth m.	3 years before July	Aug.	Sept.	Oct.	4 years before July	Aug.	Sept.	Oct.
20	—7	49	35	—3	—3	28	50	—4
30	36	52	24	11	19	49	59	28

This relationship may be explained by the effect of the ingoing current upon the plankton production. The salinity becomes high when the current is strong and more nutrient salts than usual are brought to the region, causing an increased plankton production, and better nutrient conditions for the larvae.

The yield of the **garfish** fishery in the Kattegat shows a significant positive correlation with the temperature of the water during the summers of 3 and 2 years before, and the yield in the Belt Sea with the temperature 2 years before (see Table 2, a and b). The displacement of 2—3 and of 2 years corresponds to the mean ages at which most garfish are fished in the Kattegat and the Belt Sea, respectively. No doubt this connection is caused by the beneficial effect of the summer temperature on the larval and the very young stages of the garfish.

Table 2.

Correlation Coefficients (× 100) between the Yield of the Danish Garfish Fishery a) in the Kattegat in 1916-40 and b) in the Belts in 1911-34 and the Surface Temperature.

a) Temperature	April	May	June	July	August	Sept.	Oct.
same year	— 9	5	35	16	26	52	21
1 year before	25	12	— 3	24	39	47	18
2 years —	24	29	4	41	39	57	27
3 — —	19	38	41	56	50	52	34
4 — —	—17	5	3	32	33	24	28

b)	Febr.	March	April	May	June	July	Aug.	Sept.
same year	27	20	2	—7	—35	7	—10	17
1 year before	11	31	5	—3	— 8	0	35	31
2 years —	26	45	45	23	20	57	55	33
3 — —	—18	16	5	—5	4	9	11	1

The catch of garfish in the Sound also shows positive correlations with the summer temperature of the water 2 and 3 years before, but the coefficients are smaller than those found for the Kattegat and the Belt Sea, the highest being 0.39 for July 2 years before (calculated for the years 1916—40). This is obviously because the catch in the Sound to a very great extent is influenced by the hydrographical conditions during the fishing year (see below).

The spawning of the **oyster** and the density of the natural stock depends very much on the summer temperature as shown by Spärck (71, 72).

2. The Distribution.

The distribution of eggs and larvae and the youngest stages of fish is influenced by the currents. The influence upon the distribution of eggs and larvae of the **plaice** was discussed by C. G. Joh. Petersen in 1903 (53). His view that the surface currents mainly carried the eggs and larvae away from the Belt Sea to the Kattegat was supplemented by A. Otterstrøm in 1906, who showed that the transport from the Belt Sea took place also towards the Baltic with the current in the lower water layer (52).

By an investigation in 1929 of the racial characters of the plaice, Johansen came to the conclusion that considerable quantities of larvae of the North Sea race were carried from the eastern Kattegat to the Belt Sea and the Baltic by the current in the upper water layer. For the years 1924—27 he found a distinct correlation between surface salinity and average number of anal fin rays in the Great Belt (38). Moreover, in an investigation of the fluctuations in the racial characters from year to year, Poulsen (65), found positive correlation coefficients between the mean numbers of anal fin rays of the 0-group and the bottom salinity at Schultz's Grund in each of the months of February, March and April. For the mean salinity in all three months he found the coefficient 0.48 (18 years). No doubt this corroborates the hypothesis of Otterstrøm and Johansen that there is a considerable influx of plaice from the Kattegat to the Belt Sea (65, p. 31).

From the previously mentioned negative correlation coefficients between the numbers of the 0-group and the salinity at the bottom (18), we must conclude that the consequence of an especially great influx is a diminution of the number of the fry. In this connection it may be mentioned that Kramp (42, p. 11) has stated that very few eggs of plaice (in contradistinction to cod eggs) were carried southwards by a considerable inflow of water through the Great Belt about the middle of March 1922.

Kramp (42) and Kändler (46) found that the numbers of **cod** eggs (and Kändler that the number of larvae) in the southern Belt Sea increased, when a strong inflow (indicated by a high salinity) took place. Kramp supposed that this showed a transport from the Kattegat and the northern Belt Sea. Kändler (46, p. 61) attributed the connection partly to an inflow of larvae, and partly to a presumed stimulating effect of a high salinity upon the spawning of the cod (and some other fishes); and because the eggs of cod (and dab) were mainly just spawned he came to the conclusion that the transport of eggs to the Fehmarn Belt was of little importance.

Poulsen, who has shown that there is a correspondence between the fluctions from year to year of the numbers of cod eggs and cod larvae in the Belt Sea, has supposed (60, p. 100) that probably considerable numbers of older larvae or bottom stages of the 0-group are brought into the Belt Sea and the western Baltic—and presumably also the southern parts of the Kattegat—when a strong inflow of salt water takes place in the spring or early summer, but it must be added that no significant correlation between the strength of the year-classes and the salinity (inflow)

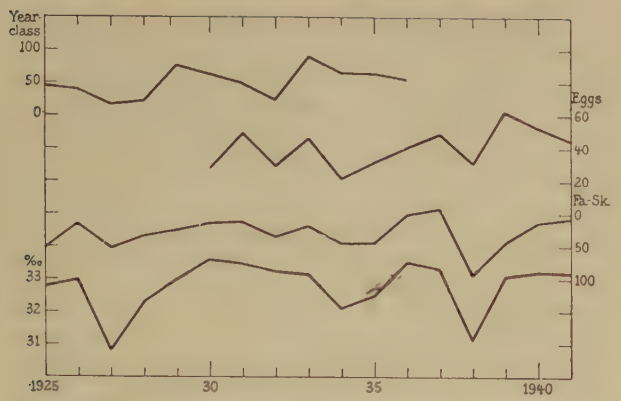

Figure 2. The quantity of dab eggs and "catch figures" compared with bottom salinity and difference of barometric pressure (see text).

has been found. He later demonstrated that other factors (the temperature and the plankton) seem to be by far more important (66, see above).

A transport by the ingoing current of the eggs and larvae of **haddock** in the Kattegat and Belt Sea in the spring of 1923 was described by A. C. Johansen (33, 35) and he also demonstrated that this was the cause of the great many haddock found in the western Baltic and the Little Belt during the following years.

C. G. Joh. Petersen (55) and H. Heidrich (11), also recorded the great amount of haddock fry and gave the same explanation. E. M. Poulsen (58, 63) showed that such inflows of haddock larvae occurred in other years too. Kändler (46) has found that the quantity of eggs and larvae of the **dab** in the Fehmarn Belt is greater when the salinity is higher than normal. As the eggs, except at the end of the spawning season, were always in the early stages of development, whether the inflow was slow or strong, he concluded that the connection between the amount of eggs and the inflow (the salinity) should be explained by a stimulating effect of a high salinity upon the spawning. It is not quite certain that this conclusion is correct, and it may be that many eggs are in fact carried in. Kändler has demonstrated that the connection between the numbers of dab larvae and the salinity is due to the transport of larvae by the current.

As a rule the stock of dabs in the Kattegat is more dense than that in the Belt Sea, and therefore we may expect that the fluctuations from year to year of the density of the stock in the Belt Sea are influenced by the strength of the inflow of water in the lower layer. From Figure 2 it is seen, that this seems to hold good. On this figure I have compared the bottom salinity at Schultz's Grund L. V., in May, June, and July, and the difference in barometric pressure between Fanø and Skagen during the half year January—June with (a) the quantity of eggs at Halskov Rev L. V. (in the Great Belt) stated by Heegaard (10), and (b) the "catch figures" calculated by Poulsen (64) for the strength of the year-classes. The latter figures are based on the average numbers of the I, II, III and IV-groups, respectively, found by the Danish quantitative fishery in the Belt Sea (when these figures have been derived from material including at least one of the I and II age-groups, the quantities of which are, no doubt, determined more exactly than the quantity of the III and IV-groups). May, June and July (according to Heegaard (10)) is the main spawning season of the dab in the Kattegat. The pressure difference at Fanø—Skagen determines the frequency of the western winds and a comparatively slight prevalence of these winds will cause a strong outflow from the Baltic which is followed by a strong inflow in the lower layer (20).

Figure 2 shows that the fluctuations from year to year in the number of eggs and also in the strength of the year-classes are negatively correlated with the frequency of western winds and positively correlated with the bottom salinity.

A good many larvae of the **saithe** also were carried to the Kattegat by the strong inflow of salt water in the spring of 1923, as mentioned by Johansen (34, 35), but far more were carried to the Kattegat, the Belt Sea and the Sound by an inflow of 1932 described by E. M. Poulsen (61, 63).

Larvae of **whiting** and **long rough dab** according to Poulsen (63) were mainly found in the years when strong inflows of salt water occurred; for **poor cod** and **Norway pout** the correspondence was not so great. The strong inflow of long rough dab larvae was deduced by P. F. Meyer from the occurrence of a large stock of commercial fish in the western Baltic (49) and the correctness of this assumption was confirmed by Meyer later on (50).

3. The Growth.

That the growth (average length) of the **cod** larvae was shown by Poulsen (66) to be correlated with the temperature in January—May is mentioned above. He thought that this was due to the temperature influencing the growth which is no doubt correct—but a delaying of the spawning time on account of abnormal temperatures must also play a part.

B. The Influences on older Fish and other Animals.

1. Mortality.

Mortality directly and indirectly caused by hydrographical factors, which plays a very great part in the egg and larval stages, is of slight importance to most of the stocks of older fishes.

(a) Mortality caused by low temperatures. It has been stated by Dannevig that in the coastal waters about Arendal fair numbers of **pollack, coalfish, cod, black goby** and other fish have been found killed by the cold in severe winters, and A. C. Johansen (39) has found that a great many different species may be found dead in the Danish waters after the melting

of the ice in such winters. This effect of the cold is mostly seen in the Limfjord and other inlets and in bays and fjords. The effect of the cold will seldom reach more than a few metres, except in the Skagerak and the North Sea where some 10 metres may be affected. Very many **porpoises** may be killed when the sea is covered with ice.

The mortal effect of the cold is clearly seen on **bottom invertebrates** in the coastal regions as described by H. Blegvad (3).

The mortality of fish and fish food is restricted mainly to small parts of the sea and therefore, in most cases, seems to have little effect upon the size of the fish stocks or their food. Thus I have shown that there is a very pronounced positive correlation between the amount of first-class plaice food present in the Limfjord in autumn and the following spring, whereas the changes during the summer are very different from year to year (15). During the cold winters in the years 1909—28, considered in the named investigation, no extraordinary reductions of the amount of food animals have taken place.

It has been suggested by E. M. Poulsen that the cold winters 1940—42 caused a very great decrease in the total yield of **eels** in the Limfjord in 1942 and 1943, and also a very great decline in the average catch of eels taken by the quantitative fishery in this region in 1940—45 (68, and in other volumes of Ann. Biol.).

From Figure 3 it is evident that the yield of the silver eel fishery in the Limfjord was a little lower than normal in 1942—43 but that this decline may be fully accounted for by the low summer temperature in these years, which has a most marked effect upon the maturing of the eels and thereby upon the yield of the fishery (cp. below, section 3). On the other hand there was in 1942—44 a distinct decline in the yield of yellow eels taken by seines, hooks and spears which might seem to correspond to the low winter temperatures two years before, and moreover it is seen that a decline of the yield, more or less, was found also about 2 years after each of the cold winters 1929, 1937 and 1947. Yet the decline in 1942—44 may be due mostly to a decline of the fishery intensity. Of the three implements mentioned the otter-seine is by far the most important in the Limfjord. During the later years of the war the seine fishery was restricted because the fuel was scarce. At the same time a fishery for mussels was remunerative and, requiring little fuel, was preferred by many of the fishermen. The great decline in the stock shown by the quantitative fishery during the years 1940—45 may be due partly to the fact that work was carried out from a small motorboat instead of the research steamer.

For the other species no lethal effect of hard winters on the fishing yield has been found from the fishery statistics. Yet there must have been a decline in some stocks on account of the cold. No doubt there has been a decrease in the yield of **sand worms** taken for bait after the severe winters but for these organisms the statistics give no information.

Many of the fishes coming here as rare visitors during the summer and autumn are killed in the winter by the cold (15). The small horse mackerel, sometimes frequent in the southern Little Belt and the adjacent parts of the western Baltic, can be killed by the cold in immense quantities, as in the winter 1949/50 (27).

(b) Mortality of older fishes caused by abnormal salinities has been observed directly in the Transition Area only in the case of the **pike**, which may be paralysed and killed in the sounds between Seeland, Falster and Møen when the winds suddenly bring salt water to this normally brackish region. In a few cases the low salinity of the inner parts of the Transition Area may be the cause of death of oceanic fishes which stray into these waters (21).

2. Migrations influenced by Hydrographical Factors.

The great coastal **herring** fishery at Bohuslän was shown by Ljungman (47) to vary fairly regularly,

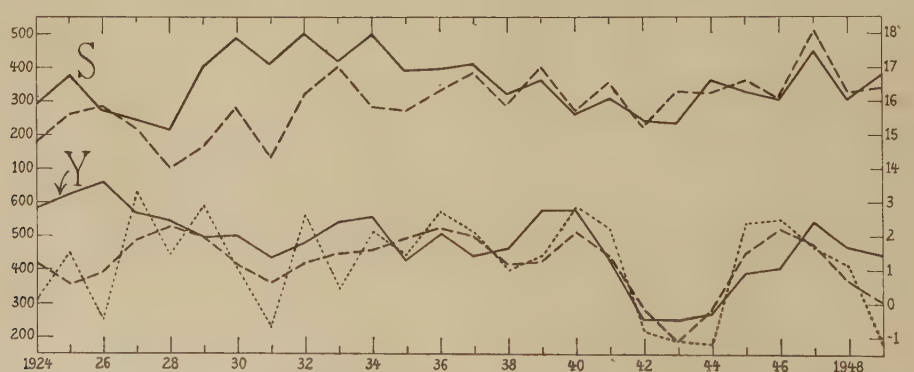

Figure 3. The yield of the eel fishery in the Limfjord in metric tons compared with the surface temperature (at Oddesund). S, silver eels caught with pound nets and weels; the broken line gives the temperatures in June, July, August, and September. Y, yellow eels caught with seines, hooks, and spears; the dotted line gives the temperatures in January, February, and March $2^1/_2$ years before the catch was made; the broken line gives the average temperature values over 3 years for the same months, smoothed in the following way: $^1/_4$ each of the temperature values $3^1/_2$ and $1^1/_2$ years before the catch was made plus $^1/_2$ of the temperature values $2^1/_2$ years before.

occurring in periods at intervals of about 110 years, and he suggested that the cause was a 55-year periodicity in the solar spots. By a very careful investigation of the information at hand LJUNGMAN proved that the main part of the herring caught off the Bohuslän coast during the periods of rich herring fishery consisted of autumn spawners, mixed to a small extent with winter and spring spawners. LJUNGMAN came to the conclusion that the autumn spawners which from October were mostly spents originated from the North Sea.

O. PETTERSSON (56, 57) found that herring came to the Bohuslän coast with inflows of salt water, and he sought for an explanation of the cyclical fluctuations in a 111-year periodicity in the current from the North Sea into the Skagerak due to fluctuations in the tide-producing forces. A. C. JOHANSEN proved that most of the herring were autumn spawners from the North Sea, and K. A. ANDERSSON has proved that, at any rate in most cases, they are identical with the Fladen Ground herring. It may seem that the secular fluctuations of the Bohuslän fishery correspond to the fluctuations given for the barometric pressure gradients at Skaw—Fanø and Copenhagen —Fanø during 1873—1934 (or the prevalence of south-eastern winds) in the second and third quarters of the year (20). The prevalent south-eastern winds during the rich Bohuslän fishery must have given rise to a strong inflow of salt water to the Skagerak and northernmost Kattegat during July—September with the effect that more herring were carried into the Skagerak from the North Sea during this period. It must also have improved the survival of the Kobbergrund herring (Table 2) and it may be supposed that the Kobbergrund herring (which are rather closely related to the North Sea autumn spawners) may have played quite a considerable part in the rich Bohuslän coastal fishery.

The autumn herring fishery in the Great Belt was proved by A. OTTERSTRØM to be influenced by temperature, the herring avoiding water with a temperature of more than 15° C., and by the inflow of salt water from the Kattegat.

If we correlate the yield of the fishery in this region in the second half of the year 1920—44 (mainly during September—October) with the salinity at Schultz's Grund L. V. we get the following coefficients (multiplied by 100):

	Temperature		Salinity	
	0 m.	26 m.	0 m.	26 m.
June	38	—30	—19	28
July	— 4	—41	21	51
August	—48	—18	53	26
September	—67	17	22	—10
October	—36	—43	10	— 5

The influence of the surface temperature is clearly shown. The correlations with the bottom temperature and the salinity may be due to their correspondence with the surface temperature but there is no doubt, also some direct influence of the salinity indicating that an inflow of salt water will carry herring to the Great Belt from the Kattegat.

It is well known that JOHANSEN has demonstrated that the yield of the **mackerel** fishery in the Skagerak and Kattegat is influenced by the hydrographical conditions previous to and during the fishing season, and that he thought it most likely that the influence was due to mackerels preferring a low temperature during spawning. In addition, I have found that the inflow of water from the North Sea carrying the mackerels into the Skagerak seems to be the principal factor (19, 26).

Figure 4 shows the correlations between the yield of the Swedish fisheries with drift-nets and trolling lines respectively, and the winds, the salinity and the temperature. The yield of the fisheries vary according to prevalence of eastern winds (they are negatively correlated with the barometric gradient Fanø—Skagen which is related to the prevalence of

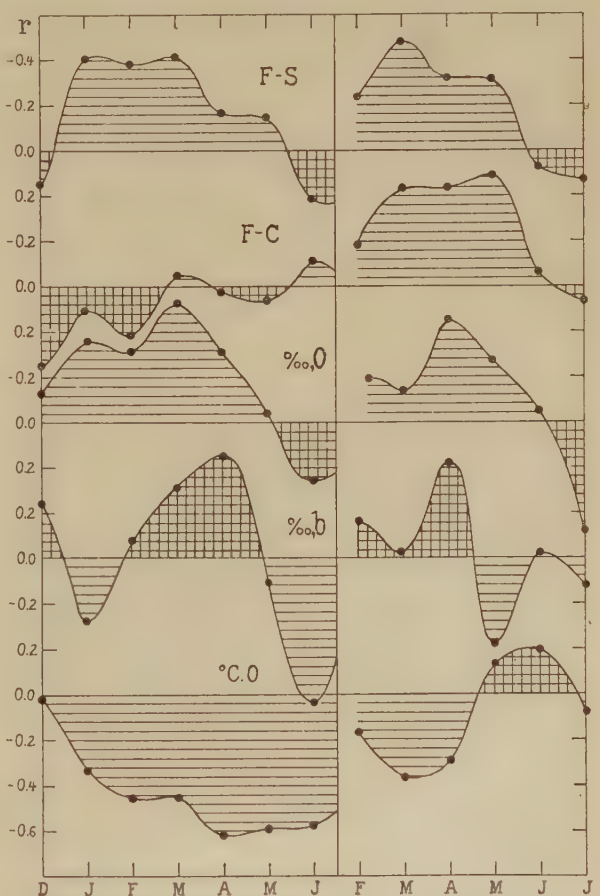

Figure 4. The yield per cutter of the Swedish mackerel fishery with drift-nets (left hand side) and with trolling lines (right hand side) correlated with the barometric gradients Fanø—Skagen (F-S) and Fanø—Copenhagen (F-C), salinity and temperature of the water in the various months. (0: at 0 m., b: at bottom). 1919—39.

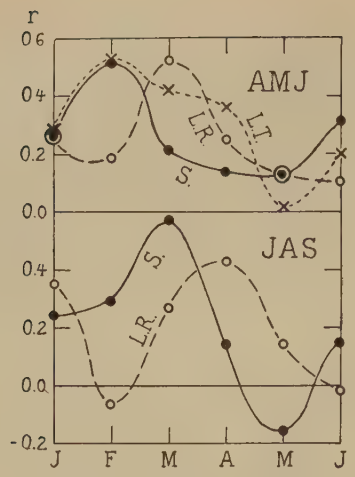

Figure 5. The catch of mackerel in pound-nets at Skagen —Frederikshavn in April, May, June (AMJ) and July, August, September (JAS), respectively correlated with the bottom temperature at the Skagen Rev L. V. (S), Læsø Trindel (L. T.) and Læsø Rende L. V. (L. R.). 1919—39.

western winds) during the months previous to the fishery seasons. The yield of the drift-net fishery, which is carried out in May—June, i. e., previous to and during the spawning, is negatively correlated with the temperature. The yield of the fishery with trolling lines, which is carried out in June—August, shows no correlation with the temperature but is influenced by the southern winds (gradient Copenhagen—Fanø) which prevent the mackerel from leaving the region, the mackerel being found at the surface after the spawning.

The yield of the pound-net fishery at Skagen—Frederikshavn does not seem to be influenced by the winds or the currents but is correlated with the temperature of the lower water layer in the winter months (Figure 5). The correlation may be due to more of the young mackerel staying in the Skagerak during winters when the temperature of the water is relatively high.

In the Belt Sea, the Sound and the Baltic the yield of the mackerel fishery is positively correlated with the frequency of northern winds in the spring and summer months (Figure 6). This is explained by the fact that these winds will diminish the normal outflow of Baltic water through the Kattegat or even give a southgoing current in the upper layer; thereby they will cause more mackerel to wander into the inner Danish waters. No doubt a cyclical variation in this wind component has caused a decrease in the yield of the mackerel fishery in these waters during recent years (21).

The yield of the mackerel fishery in the Sound is positively correlated also with the frequency of western winds during the spring and early summer carrying the water and the mackerel towards the east (Figure 6).

At the same time an increase in the frequency of western winds during the summer has had the effect that in recent years more mackerel penetrate into the inner parts of the Baltic than was formerly the case (21). For the Sound I have found a positive correlation between the temperature in late autumn and the yield of the mackerel fishery, no doubt on account of the mackerel staying longer in this region when the water is warm, while they leave it earlier in the years when the water is cold (17).

For the yield of the **tunny** fishery in the Skagerak—Kattegat I thought some years ago that I had found a positive correlation with the frequency of western winds during the early summer (13), but in recent years no such connection existed.

The **garfish** normally enter the Kattegat in April and leave the Danish waters in September—October. The yield of the garfish fishery in the Kattegat as distinguished from the mackerel fishery is only slightly influenced by the strength of the ingoing current in the spring. On the other hand the yield in the Sound shows the following significant correlations (for the years 1916—40) with the western and northern winds (coefficients multiplied by 100):—

	Barometric gradient in							
Yield of fishery correlated with gradient.	JFM	FMA	MAM	AMJ	MJJ	JJA	JAS	ASO
Fanø-Skaw..... (western winds)	50	71	75	83	45	17	—19	—15
Fanø–Copenhagen (northern winds)	57	70	68	82	15	—41	—77	—38

The number of **cod** larvae was found by E. M. Poulsen to show a positive correlation with the salinity of the lower water layer in the preceding November —December which he thought might be explained either by an indrift of large cod positively correlated with the inflow of water, or by these cod staying longer

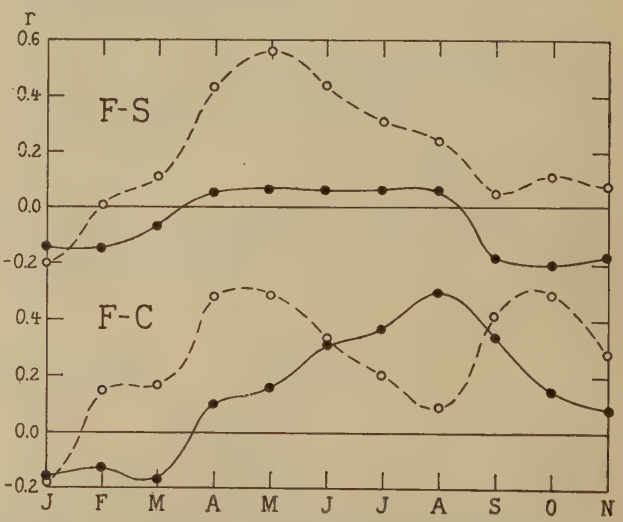

Figure 6. The yield of the Danish mackerel fishery (1919 —39) in the Belt Sea and the western Baltic (full lines) and in the Sound (broken lines) correlated with the barometric gradients Fanø—Skagen (F-S) and Fanø—Copenhagen (F-C) in three-month periods. J = December, January, February; F = January, February, March, etc.

in the inner Danish waters when the salinity is higher than normal (66). It might possibly be explained also by the fact that the strength of the inflow of salt water in the winter months, which brings with it nutrient salts, will be one of the factors determining the production of plankton nourishing the cod larvae the following spring. JØRGEN KNUDSEN (41) noted an increase in the amount of **whiting** found by the quantitative fishery carried out from the Danish Biological Station and an increase in the yield of the Danish whiting fishery in our inner waters during recent years and ascribed this to an increase in the inflow of salt water carrying an increasing number of 0- and I-group whiting from the North Sea and the Skagerak to the inner Danish waters. Although, as mentioned above, a good many whiting larvae are carried to the region in years with a strong inflow of water during the spring and early summer, this seems to be less important for the size of the commercial stock than the indrift of young fish (41).

The season for the occurrence in the Transition Area of fish and other animals as visitors from the ocean is usually determined by the temperature, and the fluctuations in their occurrence from year to year are in many cases strongly influenced by the strength of the inflow of water from the North Sea (21, 31, 34, 43, 44, 46, 48).

3. Growth and Quality influenced by Hydrographical Factors.

The quality of the small **herring** in the Kattegat and the Belt Sea from year to year is correlated with the salinity of the lower water layer in the preceding months. This may be explained by the nutrient salts of the inflow stimulating the production of pelagic organisms on which the herring feed (28).

The fat content of the adult North Sea herring caught in the Skagerak during the winter was correlated with that of the herring fished in the western North Sea the previous autumn but the former values were lower. The fat content of the herring in the North Sea seems to depend on the inflow from the north during the previous months bringing an amount of nutrient salts in proportion to the strength of the inflow (the salinity) (28).

It has been shown by H. BLEGVAD that the growth (average length) of the 0-group **flounders** in the Belt Sea depends upon the temperature (4). The growth of the **plaice** in the Belt Sea depends to a very high degree on the temperature of the water (23, 24).

4. Maturation.

The maturation of the **eel** is influenced by the temperature as shown by J. P. JACOBSEN and A. C. JOHANSEN (13) who proved that the yield of the silver eel fishery in the Danish waters was positively correlated with the summer temperature of the water, which they explained as a consequence of the fact that more yellow eels must change to the maturing stage during warm summers than during cold summers. An anomaly of 1° C. corresponds to 15—20 % anomaly of the yield (26). For the Limfjord the connection is shown in Figure 3.

C. Other Biological Influences.

Further influences have been ascertained. Some of them may act, directly or indirectly, upon the fluctuations of the quantity or the quality of the stocks. A few may be mentioned here:—

The time of spawning is altered when the water is especially warm or especially cold. This has been noted by many authors and for many different fishes: for the cod, the plaice, the flounder and the dab. Yet the temperature during the main spawning season of a fish may differ some few degrees from one year to another. HEEGAARD (10) reports that in most years the spawning of the cod will reach its maximum when the vertical difference of the temperature in the discontinuity layer is especially great. For the flounder he has found that lesser fluctuations in the temperature do not seem to have any influence on the amount of eggs, but that temperatures of less than 2° C. seem to delay the spawning very much.

The number of *anal fin rays* of the plaice in the Belts and the Baltic has increased along with temperature during recent years (38), and a similar change has been found for the dab (22). Also for the mean number of anal fin rays of the plaice and the dab in the various years I have found distinct positive correlations with the temperature (25).

An increased rate of *sex-changes* of the oyster in the Limfjord in warm summers has been described by R. SPÄRCK (44).

D. Conclusions.

A great many more influences of hydrographical factors exist. It is of special importance to determine them exactly so that it becomes possible to determine their effect on the fish stock and thereby on the fishery numerically. It may be interesting to know that there are, or seem to be, connections or dependences, but if we wish to give predictions of the yield of a fishery of real value to the industry, or when we do not know if a decline in the density in a stock of fish is due to the fishery, we must know the size of the effect of hydrographical factors exactly in order to calculate the size of the fluctuations in the density caused by natural factors.

In this respect a great field of work is before us.

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Abbreviations used for the series:

Journ.: Journal du Conseil.
Medd.: Meddelelser fra Kommissionen for Havundersøgelser, Ser. Fiskeri and Medd. f. Komm. f. Danmarks Fiskeri og Havundersøgelser, Ser. Fiskeri.
Rep.: Report of the Danish Biol. Stat.
RPV.: Rapports et Procès-Verbaux.

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9.

Fisheries Hydrography in the Baltic.

By

H. Alander.

The Baltic, being the world's widest area of brackish water, is very suitable for studies of the influence of the hydrographic conditions on the fishery, particularly concerning the influence of the salinity. The salt water coming in through the entrance of the Baltic penetrates as a bottom current into this area and as it proceeds becomes more and more mixed with water of lower salinity. Accordingly the basins of the Baltic show very great differences in the salinity of the water in their deep parts. In the Bornholm Deep the salinity of the bottom water is about 15—16 ‰, east of Gotland it is about 12 ‰, west of Gotland 10—11 ‰, in the Sea of Bothnia about 6 ‰ and in the Bay of Bothnia only about 4 ‰. The salinity of the surface water increases from about 1—2 ‰ in the northernmost part of the Bay of Bothnia to about 8—9 ‰ in the southern Baltic. Only comparatively few species of sea fishes can propagate and live in the brackish water of the Baltic and the number of them decreases as the salinity decreases.

In recent years great changes in the Baltic fishery have taken place, and in some cases these changes seem to be due to changes in the hydrographic conditions. During the war the fishery in the Baltic increased very much, no doubt due partly to favourable commercial conditions. Particularly the cod fishery gave enormous catches, and it had been supposed that the stock of cod would be overfished very soon. It was found, however, that the stock was so large and its recruitment so strong that no signs of overfishing so far have been traced. The cod fishery in the Baltic has, since the end of the war, been very great; in Europe second only to the Norwegian fishery.

Hessle has given a report on the increase of the stock of cod and the cod fishery in the Baltic (Ann. Biol. Vol. IV, 1947) but he gives no explanation of the great increase of the stock. The investigations of the Baltic cod have shown, however, that the recruitment of the stock was very strong in the early 1940's. In the years 1942—1944 the catches, particularly with herring-trawls, contained enormous quantities of small cod, obviously constituting the chief part of the stock (Alander, Ann. Biol., Vols. II—IV). In the years 1944—1946 the contribution of the 0-group to the stock was rather small, at least compared with the preceding years, and the fishery was chiefly based upon the strong year-classes from the beginning of the 1940's. In 1947 the 0-group again was very strong and that year-class now constitutes the chief part of the stock of cod (Alander, Ann. Biol., Vols. IV—VI).

The salinity seems to have a great influence on the strength of the year-classes, as they have been strong in periods when the salinity has been high. In the years 1926—1936 the salinity in the Bornholm Deep seems to have been about normal. In 1937, however, the salinity rose to more than 17 ‰, and this was repeated in the years 1940, 1942 and 1943. In the years 1944—1946 the salinity was again rather low, but in 1947 it thus increased to the extremely high value of 18.43 ‰. Consequently the fluctuations of the salinity correspond with the fluctuations of the strength of the year-classes of the cod.

Also the salinity has been rather high in the central Baltic during the last decade, but the fluctuations have not been so strong as in the Bornholm Deep (Alander, Ann. Biol., Vols. II—VI). The stock of cod has also increased very much in this area and cod are now found in great numbers in shallow water, too, which was not the case earlier (Hessle, Ann. Biol., Vol. IV). The inflow of water with comparatively high salinity to the central Baltic from the Bornholm Basin seems to have been favourable for the recruitment of the stock of cod in that area. In the 1940's no investigations with trawl were carried out in the central Baltic and consequently very little can be said about the contribution of the 0-group to the stock in this area. Probably the recruitment of the stock was rather good during that period, but there may also have been a migration of adult cod from the southern Baltic, as tagging experiments have shown that the cod sometimes makes long wanderings in the Baltic.

In the Sea of Bothnia the salinity is low, though sufficient at least for the adult cod. The reproduction

of the stock is obviously not very good here as young cod are seldom seen, but in the last decade some small specimens have been caught in herring nets, possibly indicating an increased recruitment. The cod is, as a rule, only found here at great depths, but in recent years catches have also been obtained in rather shallow water, even in the northern part of the area. The stock of cod has obviously increased in this area (Hessle, Ann. Biol. Vol. IV; Alander, Ann. Biol. Vol. VI), and this is propably due to the higher salinity which has been observed here during the last decade.

The increased salinity seems also to have been favourable for other species of fish which normally are rare in the Baltic. In the 1940's whiting often constituted a considerable part of the catches in the Bornholm Deep. Particularly after the strong influx of water with high salinity in 1947 small whiting were often more abundant than young cod in the trawl-catches (Alander, Ann. Biol. Vol. IV). At the same time horse mackerel and long rough dab appeared in the southern Baltic, which is very remarkable and no doubt due to the increased inflow of water from the Kattegat.

In the Sea of Bothnia the stock of sprat has increased very much in recent years and large shoals of spawning sprats have frequently been found along the Swedish coast. As young sprat formed a great part of the catches, it is probable that the recruitment of the stock has been rather good in recent years, which may be due to the increased salinity.

Some observations as to the influence of the **temperature** on the fish have been made in the Baltic. The hard winters in 1940—1942 were accompanied by very low temperatures of the water in the southern and central Baltic. Particularly in 1942 the temperature in the intermediate water-layers of the Bornholm area was extremely low, which seems to have had a great effect on the growth-rate of the herring. K. A. Andersson (Ann. Biol., Vol. II) found that the winter-ring of the herring-scales was very narrow for the year 1942 but was broader for 1943 when the temperature had risen again.

In recent years some investigations have been made as to the behaviour of the Baltic herring in winter and its dependence on the temperature of the water. In summer, when the upper water layers have a temperature of more than 12° C., the herring is found in the boundary between the warmer and colder water. This fact has long been known, and the fishermen place their nets in that boundary after having determined the temperature of the water layers. But it seems as if the herring not only dislikes too warm water, but also too cold. In recent years the winter herring fishery in the central Baltic has been restricted to a rather small area off Häradsskär Lighthouse on the Swedish east coast. In 1950 and 1951 investigations were carried out in January in the central and southern Baltic, and they seem to have given a clue to this aspect as the behaviour of the herring. The water of the archipelago was very cold, generally about 1° C., from the surface to a depth of about 50 m., and there no herring could be traced. In some small basins, however, the bottom water was rather warm, about 3°, and there the echo-sounder revealed herring shoals, which in some cases could be caught with the pelagic trawl. Off Häradsskär, however, rather large shoals of herring were found in fairly shallow water, but there the water had a comparatively high temperature, about 3.5° C. The area with warmer water was surrounded in NW., W. and SW. by cold water. The herring was found just outside the boundary between the cold coastal water and the warmer water of the open sea. It seems, as if the herring leave the coastal region, when the temperature reaches too low values.

There are, no doubt, great possibilities for studies on fishery hydrography in the Baltic, not only concerning the influence of the salinity and the temperature. The basins of the Baltic show great differences as to the content of oxygen and nutrient salts in the water, but the resources for effective investigations have unfortunately been small. Increased investigations in the Baltic will not only be of great interest for science, but may also be of the greatest value for the fishery in this area.

10.

On Parallelism in the Year-Class Strength of Seasonal Races of Icelandic Herring and its Significance.

By

Hermann Einarsson.

Since Hjort (1914) in his well known work "Fluctuations in the Great Fisheries of Northern Europe", documented the importance of the variations in the strength of the year-classes of fishes, an awe-inspiring number of age analyses have been carried out. All economically valuable species of fish in north-European waters have been treated in this way and already the results have partially justified this great effort, for a close correlation between the strength of the year-classes and the yield has in some cases been convincingly established; in other cases no clear-cut answers could be obtained, mainly because of the lack of data regarding fishing effort and its effect upon the stock of fishes, and also because the significance of environmental conditions for the fish migrations could not be definitely evaluated.

With regard to one of the best known stocks of fishes, the Arcto-Norwegian stock of cod, Rollefsen (1948) states:

"It is well known that the Norwegian cod fishery has always displayed very strong fluctuations, and the investigations of recent years suggest that at least three different causes of these fluctuations may be distinguished. We find that annual fluctuations may be related to meteorological and hydrographical conditions during the actual fishing season, and fluctuations of 3—5 years' duration can be traced back to the size of definite year-classes, while fluctuations of about 20 years' duration are probably due to the fact that the stock shrinks or expands over an extended period."

The results of herring investigations during recent years are in close agreement with Rollefsen's conclusions. The annual fluctuations seem to be caused by hydrographic and meteorological factors and these will be of decisive importance when the stock strength is on a high level. This applies to the Norwegian stock of herring during recent years (verbal information from Devold). On the other hand, when the stock strength is low owing to poor year-classes during a number of years, the annual fluctuations appear on a lower level, but are nevertheless distinct, although not of decisive importance for the output because the stock strength is now the major factor. The present author has maintained (Einarsson 1949 a, 1950 a) that this applies to the Icelandic stock of herring during recent years.

Our fishery biological aims thus have three important aspects:—

1. Investigation of the causes of annual fluctuations, which are mainly hydrographic as far as the spawning stock is concerned, and hydrographic and biological when we are dealing with the food migrating phase.
2. The assessment of year-class strength by means of age analyses and comparison with the yield, together with investigations of the causes of rich and poor year-classes.
3. Investigations of the causes of long-termed fluctuations.

The present paper deals with the second aspect.

The age distribution of the seasonal races of Icelandic herring during 1947—1949.

The age distribution of the two seasonal races of the Icelandic herring has recently been described in detail by the present writer (Einarsson 1950 a, 1950 b). The general result of these studies can be seen from Figure 1. It is quite evident that during 1947—1948 and again during 1949 there is a distinct correlation between the strength of the year-classes of spring spawners and summer spawners respectively. This correlation can be formulated as a general rule as follows:—

The relative strength of a year-class of summer progeny corresponds to the relative strength of a year-class of spring progeny the following spring.

During the years 1947—1948 several year-classes were adequately represented in the catches. The dominant components were summer spawners of the year-class 1943 and spring spawners of the year-class 1944. Of older year-classes the most conspicuous were summer spawners from 1938 and spring spawners from 1939. These year-classes were dominant during 1943—1945.

In the first half of 1949 a great change occurred in the composition of the herring stock visiting the

southern coastal waters of Iceland. Two year-classes, the summer spawners of the year-class 1944 and spring spawners of the year-class 1945, which had not hitherto been of great importance, became dominant in the catches. Their strength now proved to be so overwhelming (about 68 %), that the older components were only poorly represented in our samples, with the exception of the two year-classes dominant during 1947—1948, which were still of some importance.

Although the observations on which the above-named general rule is based cover only three years, the evidence is conclusive enough to justify its formulation. Further investigations are now in progress to test its dependability both as regards older material in our possession and more recent material sampled during 1950. However, it seems evident that while the strong year-classes of 1944 and 1945 are still vigorous, only a few year-classes of summer- and spring-spawning stock respectively can be compared as to relative strength. Older material seems more satisfactory in this respect, as a greater number of year-classes are adequately represented in the same samples. On the other hand, the methods of race determination were previously rather imperfect, which considerably endangers the reliability of the results.

On the significance of the parallelism in the year-class strength.

The inference to be drawn from the parallelism shown has a bearing upon the fundamental questions concerning the causes of rich and poor year-classes. If we assume that some external factors (temperature, salinity, food or availability of food at a certain time, micro constituents of the sea water etc.) are responsible for the intensity of spawning and the growth of the larvae until the critical stage in the herrings' life-history is passed, then the logical inference from our observations must be that these factors remain relatively stable from July of one year (when the

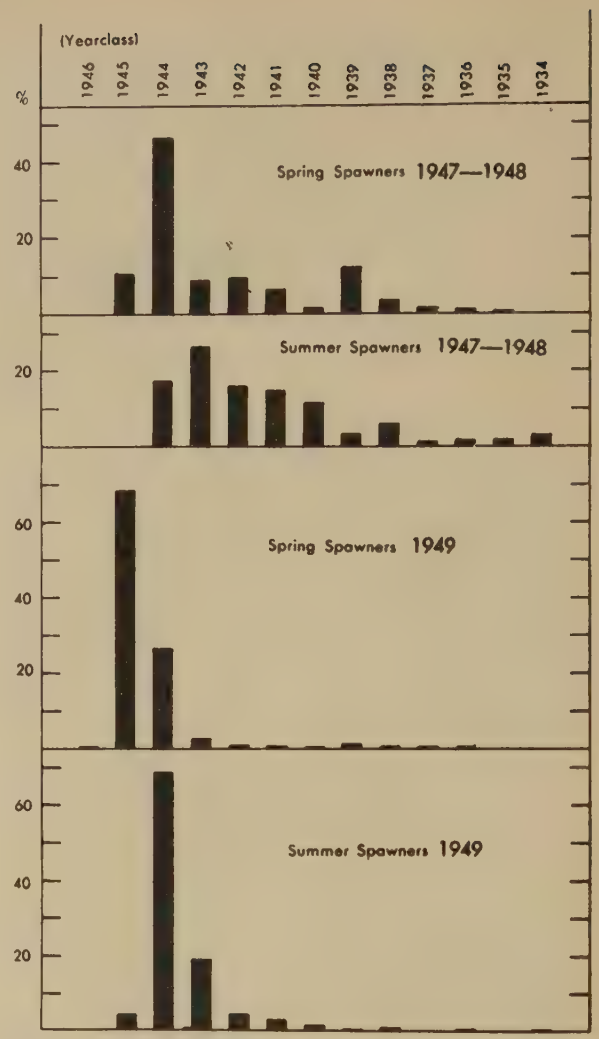

Figure 1. The age distribution of Icelandic herring during the years 1947—1949.

Mean Vertebral Numbers of Year-Classes of Icelandic Herring during 1947—48 and 1949.

Race Year-Class	No.	M	δ	m	No.	M	δ	m
		Spring Spawners				Summer Spawners		
				1947—1948				
1945	309	57.188	0.621	± 0.035	—	—	—	—
1944	1382	57.245	0.619	± 0.017	585	56.874	0.727	± 0.030
1943	240	57.217	0.628	± 0.041	877	56.968	0.744	± 0.025
1942	265	57.079	0.613	± 0.038	520	56.950	0.624	± 0.027
1941	180	57.072	0.580	± 0.043	488	56.842	0.620	± 0.028
1940	38	57.368	0.716	± 0.115	385	56.847	0.611	± 0.031
1939	344	57.288	0.422	± 0.023	96	56.844	0.546	± 0.056
1938	118	57.220	0.585	± 0.054	179	57.061	0.678	± 0.051
				1949				
1945	1833	57.223	0.463	± 0.011	174	56.868	0.620	± 0.047
1944	703	57.272	0.605	± 0.023	2934	56.982	0.570	± 0.011
1943	—	—	—	—	797	56.903	0.588	± 0.021
1942	—	—	—	—	179	56.939	0.644	± 0.048
1941	—	—	—	—	121	56.876	0.569	± 0.052

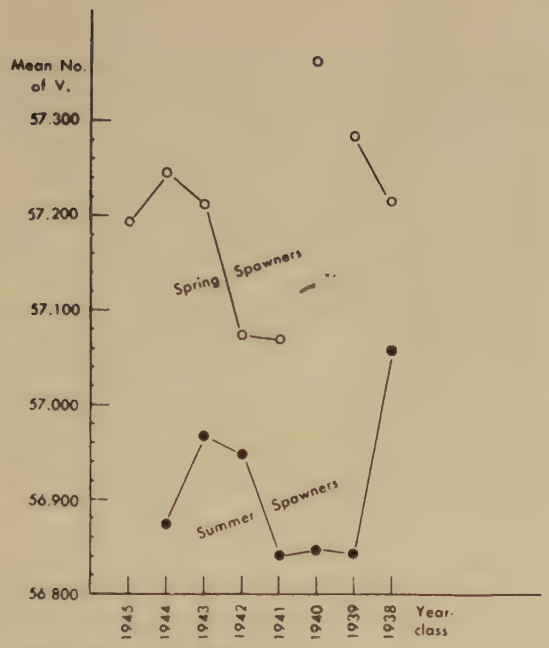

Figure 2. The mean vertebral numbers of different year-classes of the Icelandic herring during 1947—1949.

summer brood is hatched) to April of the next year (when the spring brood is hatched).

On the other hand, these factors must evidently be subjected to variation from May to the middle of July. In other words the potential fertility of the water masses alters during this period. The question can now be asked: What factors are stable from July of one year to April of the next and subject to variation from May to July?

On the relationship between the mean vertebral number of the year-classes.

The mean vertebral numbers of spring and summer spawners differ significantly (FRIÐRIKSSON 1949, EINARSSON 1950 b). During recent years the mean vertebral numbers of the two respective races have been very stable, the summer spawners having means between 56.93 and 56.98 vertebrae and the spring spawners means between 57.19 and 57.34 vertebrae. Calculations of the mean numbers for the different year-classes are shown in the table on p. 64. The standard deviation (δ) and the standard error of the mean are also shown.

The graph in Figure 2 shows the variation of the mean vertebral numbers for the different year-classes encountered during 1947—1948. It will be seen that there is a very distinct relationship between the two respective races as was experienced with regard to the variation in the strength of the year-classes, i. e., a high vertebral number of a summer brood corresponds to a high vertebral number of the following spring brood etc.

However, this relationship was not found in our material for the year 1949 as will be seen from the table. As already mentioned, only two sets of observations can with advantage be compared during this year, because of the overwhelming dominance of four year-classes, spring spawners from 1944 and 1945 and summer spawners from 1943 and 1944. Now we can expect some percentage error in the race determination, which was carried out by means of the otoliths, and it might be surmised that this error was reflected in the vertebral number. However, it seems not to be the case. As previously shown (EINARSSON 1950 b) the race determination must be considered wholly reliable during the months October to December and if we compare the vertebral number of the year-classes encountered during these months with those calculated for the whole material we get the following figures:—

Year-Class	Total	October—December
	Summer Spawners	
1943	56.903 ± 0.021	56.888 ± 0.044
1944	56.982 ± 0.011	56.958 ± 0.023
	Winter Spawners	
1944	57.272 ± 0.023	57.241 ± 0.041
1945	57.223 ± 0.041	57.192 ± 0.015

It will be seen that the mean vertebral numbers are lower in October—December but the figures show exactly the same trend. Accordingly we must conclude that errors in the race determination do not cause the absence of the correlation during 1949.

There is at present general agreement among fishery biologists that the vertebral number is primarily influenced by temperature. The correlation in the vertebral numbers established for the years 1947—1948 therefore indicates that during the period in which the year-classes in question were hatched, temperature was one of the factors which varied together with the factors affecting the year-class strength. On the other hand the observations from 1949 seem to indicate either that this is not a general rule or that the sampling during 1949 did not give a true mean vertebral number. More investigations are necessary before any further conclusions can be drawn.

On the age of the water masses.

With the exception of GUDMUNDSSON's studies on the phytoplankton during the year 1938, which will be discussed below, the Icelandic coastal waters have never been investigated at regular intervals during a whole year.

In connection with the problems discussed in the foregoing our data are rather meagre. But these may perhaps be of interest if we try to formulate a working hypothesis as to what factors are involved in deciding the year-class strength.

We might first ask: Is there any hydrographic evidence that a renewal of the water masses takes place during the period May to the middle of July? *A priori* we should expect this since the environmental factors are obviously liable to alteration during this period.

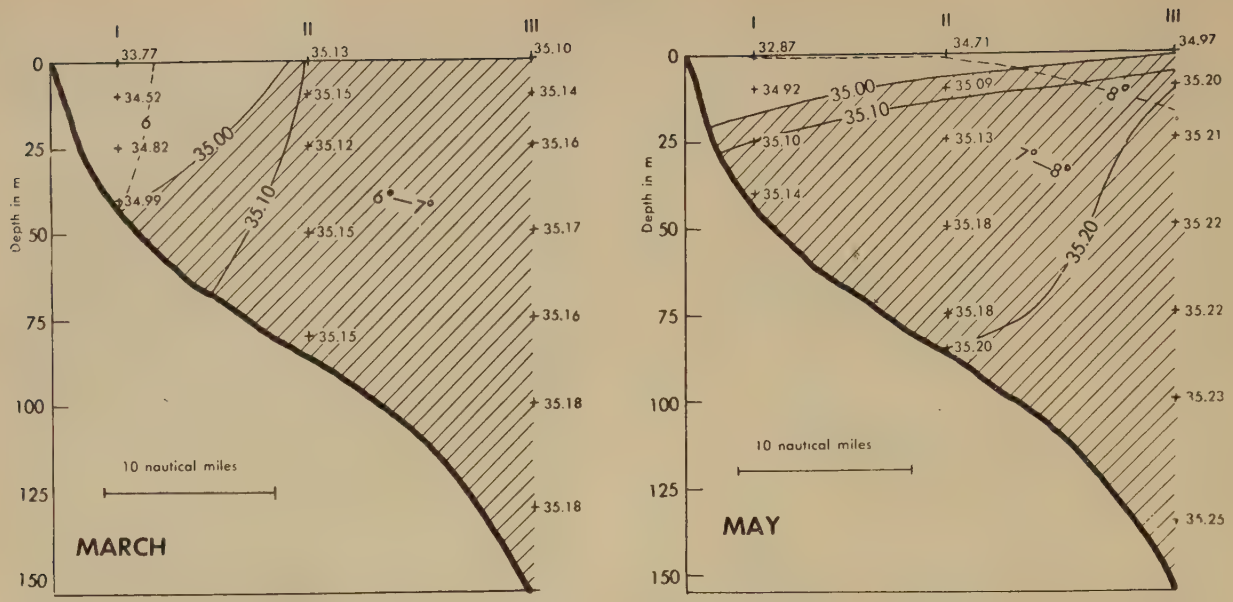

Figure 3. Average salinities and temperatures in the Selvogsgrunn section during March and May respectively.

The most complete set of hydrographic data refers to two stations situated in Faxa Bay on the south-western coast of Iceland. Coastal water, a mixture of fresh water brought from land and the Atlantic water (salinity $> 35\ ^0/_{00}$), is found in these localities. But if we examine the bottom salinities at these stations, as shown by means through many years, a definite trend appears (vide Einarsson 1941, Figure 4, p. 8). We find that the Skagi station, situated at the southern entrance to the bay, has the highest salinities in June—July, while the Akranes station situated in the inner part of the bay, has the highest salinities in July—August. These salinities come very near to the values typical for Atlantic water, and indicate in fact, that the influence of the oceanic water mass is strongest during these periods.

We also have some observations from the Selvogsgrunn area, the most important spawning grounds of the Icelandic herring. Two graphs (Figure 3) show the average conditions in the Selvogsgrunn section during March and May respectively. The observations on which the March means are based were made in the years 1934, 1935, 1936, 1947, and 1948. The May observations were made in 1934, 1935, 1936, 1937, 1939, and 1948.

It will be noticed that there are clear differences. On Selvogsgrunn I, where no Atlantic water was present in March, this type of water had reached the station during May, from 25 m. depth and downwards. If we consider Selvogsgrunn III, it will be seen that the salinity values increase from March to May, which indicates that a renewal of the water mass as a whole has taken place.

During investigations on the distribution of post-larval stages of herring, which the present writer made in 1948, the Selvogsgrunn section was worked four times in the period March—August, and the data are shown in Figure 4. These observations substantiate the conclusion stated above. The shoreward movement of the isohalines is here clearly demonstrated, e. g. in May the $35.20\ ^0/_{00}$ isohaline lies at Selvogsgrunn II, while it did not enter the section at all in March.

It has thus been possible to demonstrate the same phenomenon at five different localities off the south and west coasts of Iceland. These increases in the salinity values seem to occur earlier off the south coast than at the entrance to Faxa Bay and latest in the innermost part of the bay. However, they occur within the period May to the middle of July, in which, according to our previous conclusions, an alteration takes place which is of decisive importance for factors affecting the year-class strength.

A corresponding increase in the inflow of Atlantic water off the north coast of Iceland was clearly demonstrated during my investigations in 1947 and 1948. With regard to the summer of 1947, Mr. U. Stefánsson, M. Sc., who has dealt with the hydrographic part of the material, concludes:—

"The observations from the spring and summer of 1947 indicate that the northern grounds were affected by a strong influx of Atlantic water about the middle of June. Atlantic water constituted an intermediate layer in the Siglufjördur-Section in late June, and it had increased in thickness by late July. The eastward extension of the Atlantic tongue was, however, not definitely known, but it had not reached Langanes in late July. In late August this tongue was strongly represented in the Langanes-Section which accordingly showed unusually high temperature and salinity values at that time. The strong and early influx of Atlantic water combined with fair weather conditions

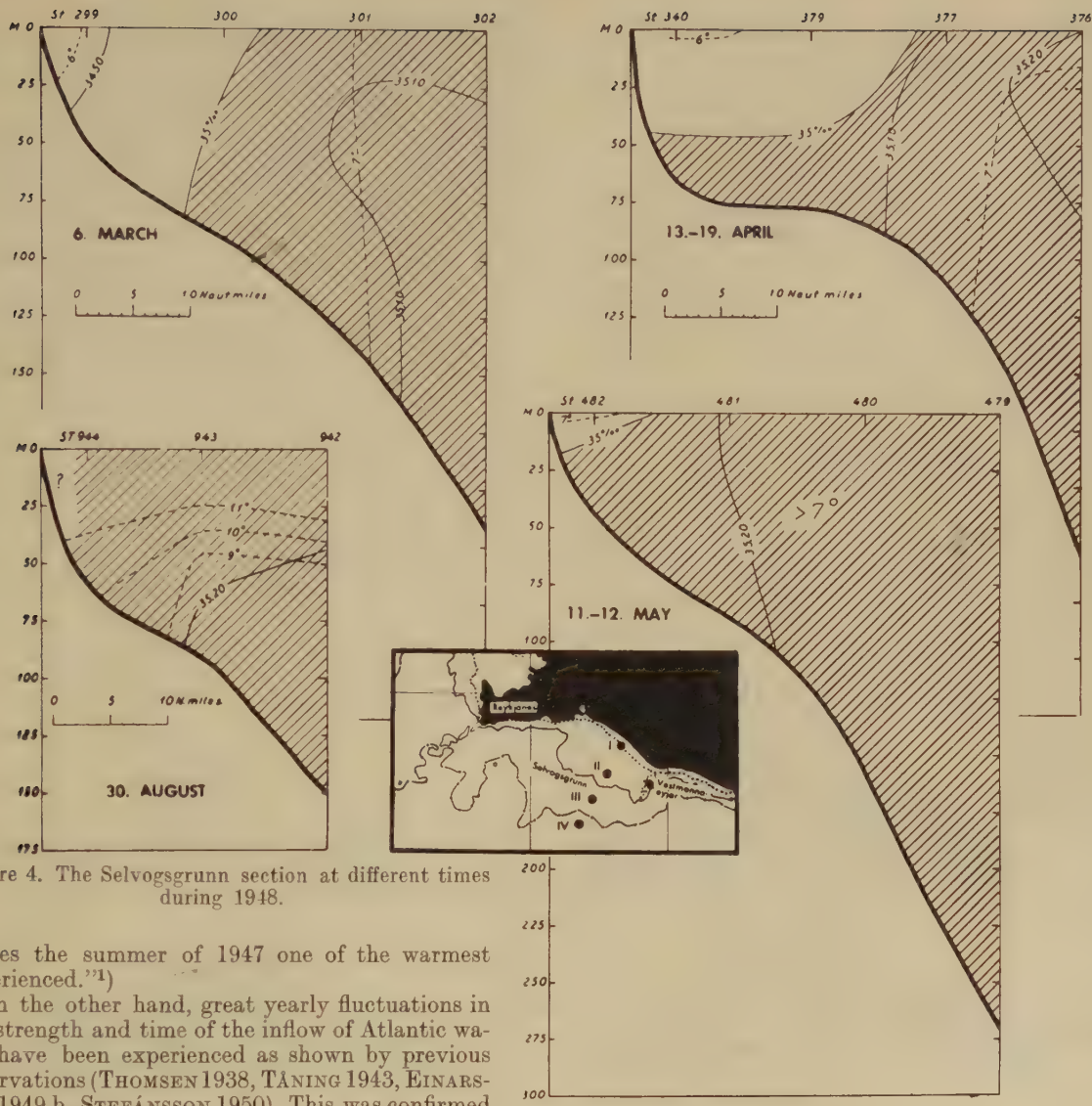

Figure 4. The Selvogsgrunn section at different times during 1948.

makes the summer of 1947 one of the warmest experienced."[1])

On the other hand, great yearly fluctuations in the strength and time of the inflow of Atlantic water have been experienced as shown by previous observations (Thomsen 1938, Tåning 1943, Einarsson 1949 b, Stefánsson 1950). This was confirmed by the investigations during the summer of 1948. Stefánsson (l. c.) states:

"The observations during spring and summer of 1948 indicate a later and less strong influx of Atlantic water than during 1947. The Atlantic water front passed Siglufjördur in early July, was observed as a thin intermediate layer off Melrakkaslétta in early August, but did not reach Langanes."

Whether there is any correlation between the strength of the inflow of Atlantic water off the north coast and the general renewal of water masses off the south and west coast is unknown at present. The answer to that question must be left to future investigations. But the facts already available seem to be exceedingly suggestive.

[1]) U. Stefánsson: Hydrographical Conditions in the Waters north and northeast of Iceland during 1947 and 1948 (unpublished).

On the role of the phytoplankton.

One of the chief links in the chain of factors affecting the size of year-classes of fishes is undoubtedly the phytoplankton. In the case of the herring it is perhaps not a primary factor, but it is an important secondary one, causing the success or failure of the zooplanktonic broods that maintain the larval stock during the critical period of the herring's life-history. The important works of Paulsen (1909), Steemann Nielsen (1935), Gudmundsson (1937) and Hentschel (1941) give a fairly good general description of the qualitative and quantitative composition of phyto-

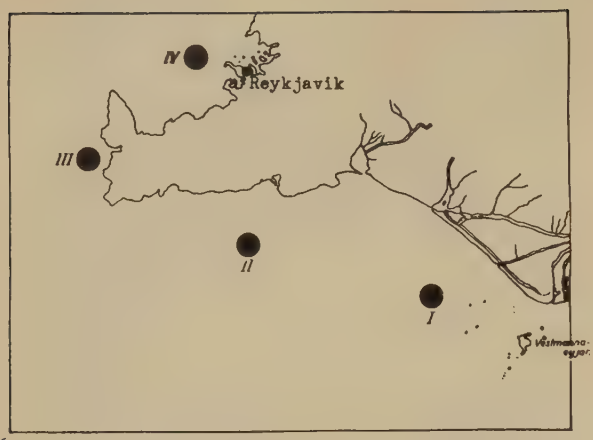

Figure 5. Localities investigated by Dr. F. Gudmundsson during 1938.

plankton in Icelandic waters although comparison of results is made somewhat difficult because of different methods employed. Another drawback lies in the fact that the collections, on which these studies are based, are not sufficient for elucidating the course of events during a whole year at a certain place, since they are based on collections of research vessels visiting the area at odd times only.

The gaps in our knowledge resulting from these shortcomings of the data available, were considerably filled by an investigation which Dr. F. Gudmundsson carried out during the year 1938. Gudmundsson studied the quantitative composition of the plankton at 4 different stations off the south and west coast and inside Faxa Bay (see Figure 5). He listed the number of plankton organisms per 5 litres of surface water according to a method previously used by Hentschel (see Hentschel 1941), and himself (Gudmundsson 1937). A preliminary report was published in 1940 (see Friðriksson 1940, Plankton Investigations p. 24, Table 9). Because of other duties Dr. Gudmundsson has not found time to publish a detailed account of his investigations, but he was kind enough to place his principal results at my disposal.

Figure 6 shows the quantitative variation of diatoms throughout the year. It will be noticed that the spring flowering of diatoms occurs in the period late

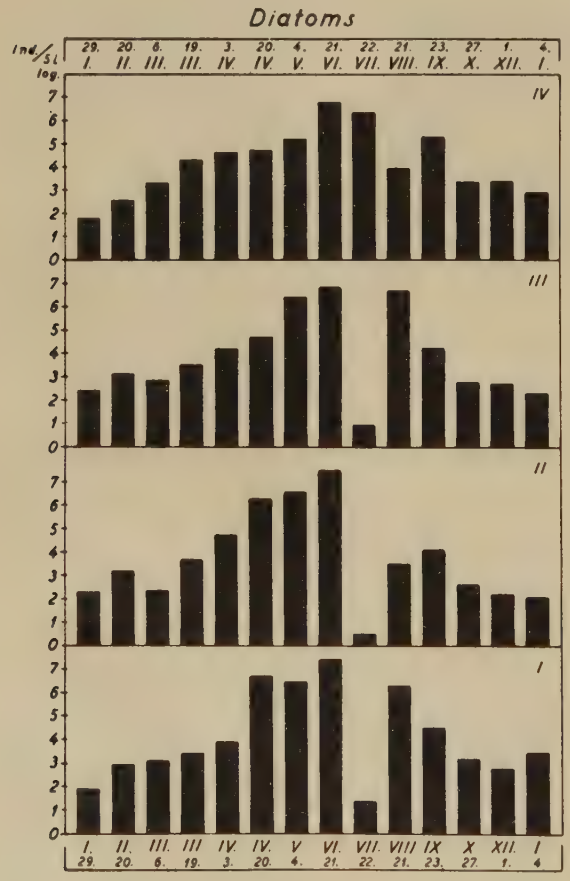

Figure 6. Variation in the number of diatoms at four different stations during 1938.

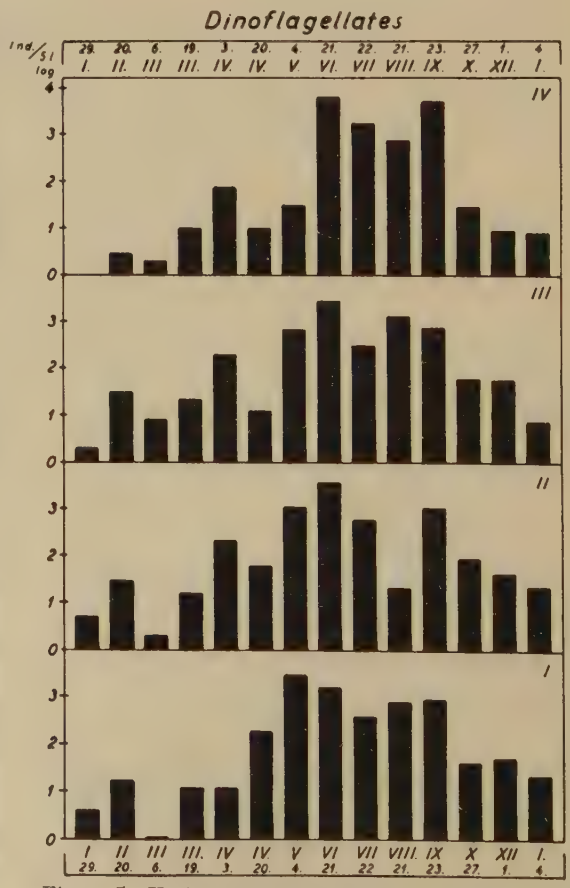

Figure 7. Variation in the number of dinoflagellates at four different stations during 1938.

April—June in the Selvogsgrunn area and off Reykjanes (I, II and III). In late July (samples taken 22. July) the diatoms vanish almost completely. A second peak, not as strong as the spring maximum, develops during autumn with maximum numbers during September. The spring outburst was correctly deduced by Steemann Nielsen (1935, 1943), but neither the extreme minimum during July nor the autumn peak could be seen from the data available to him. However, these phases were recognised by Paulsen (1909) and Gudmundsson (1937).

Figure 7, constructed in the same way, shows the variation in the number of dinoflagellates. In this group also the two maxima are clearly seen, but they occur later in the season and are not as pronounced as in the case of the diatoms.

Recently evidence showing a very similar sequence of events was secured from an area situated about 200 nautical miles south of the coastal waters of Iceland, viz., from the weather station "Item". Position 60° 00′ N., and 20° 00′ W. (Corlett 1950). Although the methods differ, Corlett basing his study on vertical hauls 50—0 m. (Standard net, silk No. 25), and calculating numbers per metre depth, the agreement between Gudmundsson's and Corlett's data is very close, and this applies to both groups studied, diatoms and dinoflagellates. He has summed up very clearly the main inferences that can be drawn from these studies. Since they seem to be of importance for comparison with Gudmundsson's observations I quote the following (Corlett l. c.):—

"Previous investigations of phytoplankton in the Atlantic south of Iceland are reported by Nielsen (1935 and 1943) and Hentschel (1936). Nielsen (1935 and 1944) says that in the Gulf Stream area south of Iceland over deep waters the phytoplankton only begins to reproduce at the end of May when production is active for a month, that plankton production for the rest of the summer is very poor, and that there is no autumn increase in production. The present investigations confirm the outburst in late spring but show that diatom production in at least one year (1949) can begin a month earlier than late May and that it lasts longer than one month, also that there is a pronounced autumn production in late September and October and even into November (1948)."

The agreement between Gudmundsson's and Corlett's observations raises many important questions regarding the causes of the phytoplankton outburst in spring and autumn, questions that will not be further discussed in this paper. But I should like to stress the importance of simultaneous observations in these two areas, as regards environmental factors, net plankton and nannoplankton.

What seems of paramount importance in connection with the problems discussed previously in this paper, is the fact, that in the spawning area of the Iceland herring, of which there are two seasonal races, there occur two maxima in the phytoplankton production, the main maximum being in May—June, i. e., in those months when the fate of two successive broods seems to be decided. It seems very improbable that this is a mere coincidence.

Following our line of thought we might expect that the zooplankton organisms constituting the food of the post-larvae of summer spawners originate in the main spring phytoplankton maximum in May—June. Assuming for example that these organisms are copepods, and we find substantiation for that in the investigations of Soleim (1945), the young generation which seems to be found in large numbers during June—July, constitutes the food for the post-larvae of the summer progeny.

In the course of the summer this generation will develop through the naupliar and copepodite stages and it winters mainly in copepodite stage V, according to Jespersen (1940). It seems a reasonable assumption that the intensity of spawning the next spring is related to the number of wintering animals and thus to the strength of the brood hatched during the main phytoplankton maximum in May—June on the one hand, and the amount of phytoplankton produced during the autumn, on the other. However, Gudmundsson's figures for the Metazoa, most of which are eggs and naupliar stages of copepods, do not indicate any noticeable rise in March and April. This is perhaps not decisive enough because these stages may be more abundant in subsurface layers of the sea, Hentschel's and Gudmundsson's sampling methods failing us in this instance. Jespersen's investigations indicate this as he states: "In April—May the new generation occurs along the south and west coasts, since not only nauplii, but also a large number of young copepodite stages are present there." (l. c., p. 7). There is every reason to suppose that the critical phase in the life-history of herring of spring progeny occurs during these two months.

Concluding remarks.

In seeking a tenable working hypothesis to account for the fact that there is a paralellism in the year-class strength of summer and spring spawners, we have made a number of assumptions to fill the gaps in our knowledge regarding the factors responsible. The aim of future investigations must be to test these assumptions and fill these gaps, and it would be premature at present to discuss in detail the data available from other areas for comparison with those here recorded. However, recent investigations can give us valuable information as to the most promising lines of inquiry.

Thus Russell (see Harvey 1950) established a correlation between the amount of phosphate at the beginning of each year and the number of fish fry (excluding clupeids) the ensuing summer. The important studies of Soleim (1942) on the causes of rich and poor year-classes, show that herring larvae go through a critical stage when the yolk sac is absorbed, and the cause of the great mortality then experienced was ascribed to lack of suitable food, which he found to be eggs and naupliar stages of crustaceans. Inter-

esting information was also gained by A. and G. Dannevig (1950), who found by numerous experiments, "that the gas tension of the sea water has considerable bearing on the survival of several species of fish larvae". Whether this applies to conditions in nature is at present not known.

These few remarks and the foregoing discussion may suffice to show that investigations on the natural causes of rich and poor year-classes must of necessity take a number of factors into consideration. This is a great obstacle to our future work in this area.

However, our present results seem to indicate that the spawning grounds of the Icelandic herring offer unique opportunities for comparing the variation of external factors with the relative strength of the year-classes resulting from each season's hatching. Such investigations might lead to important results of general significance.

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11.

Brood Strength Fluctuations in the Sprat.

By

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I. The English Sprat Fishery.

In this paper brood strength fluctuations in the sprat fishery for the east coast of England are associated with inferred movements set up by the local wind. This method of attack on the problem of brood fluctuations arose from the ideas on fishery hydrography expressed from the English side at the 1950 meeting of the International Council for the Exploration of the Sea at Copenhagen, and has been used by the author in association with J. N. Carruthers and A. L. Lawford to investigate the haddock, herring, plaice and cod of the North Sea.

The figures used to represent the sprat broods have been estimated from the qualitative evidence supplied by Robertson in the Lowestoft Fishery Investigation Series II, Vol. XVI, No. 2, 1938, and are the year-class strengths relative to 1929 taken as 10. The wind data are those for the Southern North Sea centred on $52^1/_2$° N., 3° E., as computed in the form of monthly cardinal components by Dr. Dietrich of Hamburg.

Considering that the spawning of the sprat reaches its peak during June, it was decided to investigate the wind conditions obtaining during the period May—July inclusive. It was found that good brood years were associated with low west wind resultants for May—July and poor brood years with high resultants. The correlation illustrating this is shown in Figure 1 and an explanation could be that the further the sprat are carried away from the east coast of England during the fry stage, the less they might be subject to the east coast fishery $1^1/_2$ years later.

To investigate the effect of north/south wind components during May—July, it was decided to correlate the resultant north/south wind component for the spawning period with the separation of the two variables shown in Figure 1. As regards the sign of the separation a positive one was said to occur when the line representing the brood values was above the line representing the wind components, the reverse being the case for negative separations. The correlation between separation and the resultant north/south component is shown in Figure 2 and regression lines have been tentatively drawn in. The explanation would

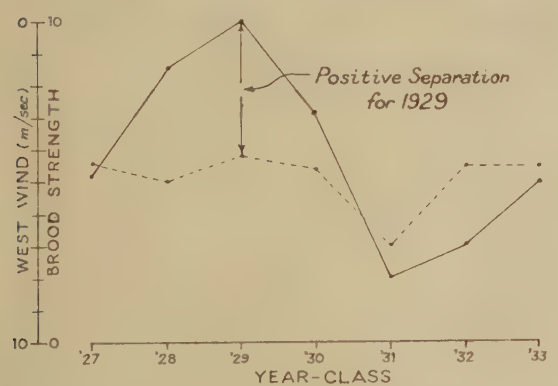

Figure 1. English Sprat Fishery — Association between Brood Strengths and Resultant West Wind Components for May—July.

——— Sprat Brood Strength.
- - - - - West Wind Component.

Note:—The west wind component scale is inverted for reasons explained in the text.

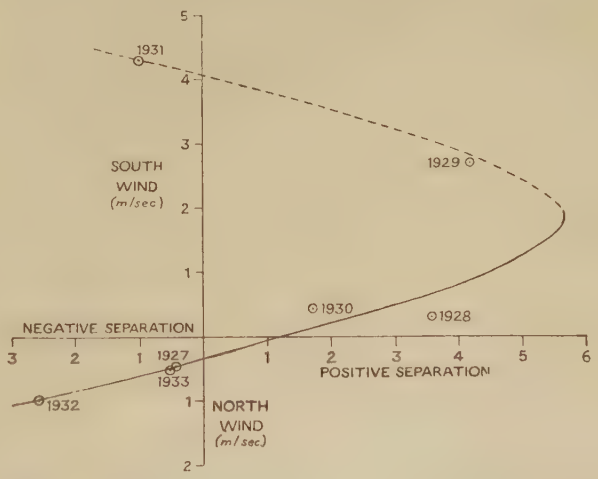

Figure 2. English Sprat Fishery — Association between Separation (vide Figure 1) and North/South Wind Component for May—July.

appear to be that for high or low south components or a north component, the sprat fry is partially dispersed outside the fishery area. The optimum value appears to be a south component of 2 m./sec. approximately which (on the evidence of wind/current relationships investigated by the author) means that the fry would be transported not more than 30 miles from the spawning area in a northerly direction. Regarding the significance of the negative regression line, it is to be noted that the slopes of the two lines are almost identical.

Using Figures 1 and 2, the following operations would be needed for prediction: —

(A) From the value of the resultant north/south component for May—July ascertain the value and sign of the separation (Fig. 2).
(B) Compute the value of the resultant west component for May—July, and subtract this value from 10.
(C) Calculate the sprat brood strength by algebraically summing the results of (A) and (B).

The above analysis is extremely tentative due to the very small number of years investigated. If reliable data were available for many more years it might be possible to attempt the prediction of sprat brood strengths. This paper however only shows the possibility of associating fluctuations in the brood strengths with wind conditions during the spawning period.

II. The Swedish Sprat Fishery.

As support for the analysis contained in Part I, it was decided to discover whether brood fluctuations in the sprat fishery for the west coast of Sweden could be explained by the use of the same analytical methods. The sprat figures are those given by A. R. Molander in the Ann. Biol. Vol. I, 1939—41, and represent the percentage contribution of I-Gr. to the stock off the Skerries Fiords during 1932—38. These figures are referred back to the year of birth and are taken as indicative of the year-class strengths. The wind data in the form of monthly cardinal components are those of Dietrich for the Central North Sea, centred on $52^1/_2$°N., 5°E., which is the point nearest to the spawning area of the sprat for which information is available.

Considering that the spawning of the Swedish sprat reaches its peak during May, it was decided to investigate the wind conditions obtaining during the period April—June inclusive. On examining the brood strength figures in conjunction with the resultant east/west wind components for the spawning months, it was found that the best year-classes were associated with a resultant west component of 1.3 m./sec. Deviations from this value, irrespective of sign, were found to be associated with marked decreases in the brood strength value. Therefore a correlation was attempted between the deviation and the value of the brood strengths. This correlation is shown in Figure 3, the actual value of the resultant east/west component for April—June being shown against each point. The explanation of this correlation would appear to be similar to that given in Part I, i. e., excessive dispersal in either an east or west direction causes too great a loss of sprat fry from the fishery area. (It is to be noted that two qualitative years, 1925 and 1939, are shown in Fig. 3 together with their east/west wind components).

As in Part I it was decided to correlate the resultant north/south component for the spawning period with the separation of the two variables shown in Figure 3 (Figure 4). All the separations are in this case negative but the axes have remained identical with those in Figure 2. If the point representing 1932 is neglected, a curve emerges which is very similar in appearance to that obtained for the English sprat fishery. The explanation of the curve is the same as in Part I although it is noteworthy that this time the minimum negative deviation occurs with a north component of 1 m./sec. Using this curve for prediction, the percentage values for 1925 and 1939 are given as 80 % and 82 % which is in good agreement with the qualitative evidence supplied by Molander. The only possible explanation of the 1932 anomaly is that some other influence, hydrographical or biological, largely affected the value of the brood strength.

Although the number of years investigated in Parts

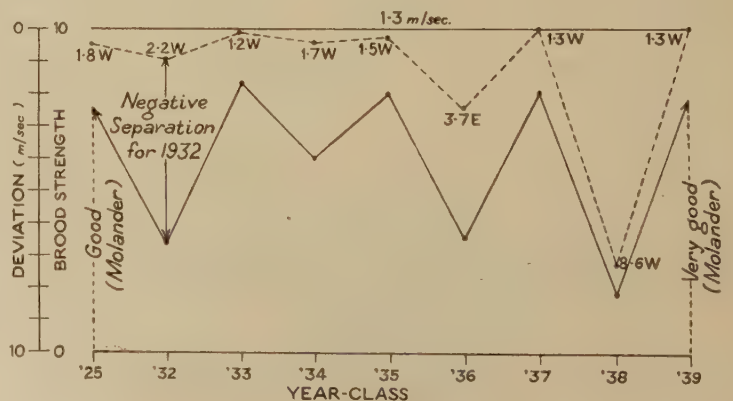

Figure 3. Swedish Sprat Fishery — Correlation between Deviation (as defined below) and Brood Strength.

——— Brood Strength (% of I-Group/10).
- - - - - Deviation, irrespective of sign, of resultant East/West wind component from 1.3m./sec. W.

Note:—The deviation scale is inverted for reasons explained in the text.

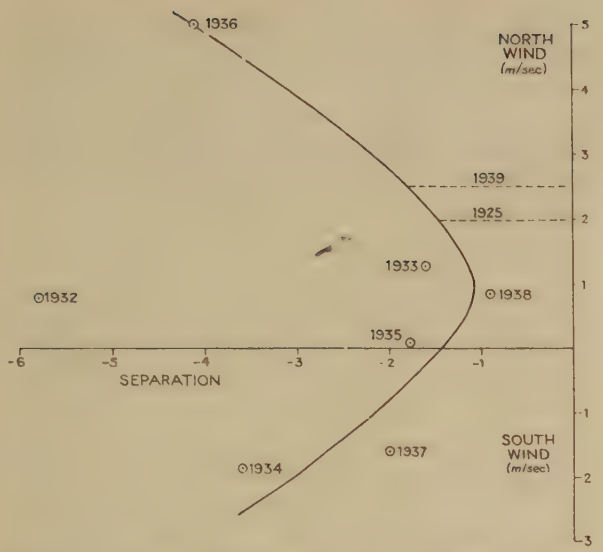

Figure 4. Swedish Sprat Fishery — Association between Separation (vide Figure 3) and North/South Wind Component for April—June.

I and II is so small, nevertheless the fact that two independent sprat fisheries respond to the same analytical methods, lends a good measure of support to the idea of associating sprat brood fluctuations with wind conditions.

Note on the Post-War English Sprat Fishery.

With regard to the fishery for the 1949—50 season, the information obtained from an echo-sounding survey and supplied by I. D. RICHARDSON in Ann. Biol. Vol. VI, 1949, lends support to the analysis in Part I. The fishery for 1949—50 would be markedly dependent on the 1948 year-class, since the year-classes immediately preceding appear to have made poor contributions to the commercial catches. The components of the wind resultant for the period May—July, 1948 are 5.3 m./sec. N., and 4.1 m./sec. W., and if these values are applied to Figures 1 and 2, the brood strength is revealed as extremely low, a result which is in full agreement with the sprat survey reported by RICHARDSON. Moreover the sprat fry would be dispersed in a SE. direction, which could be the reason for the main sprat shoals being discovered off the French, Belgian and Dutch coasts $1^1/_2$ years later.

12.

The Influence of Hydrography on the Bear Island Cod Fishery.

By

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Note:—The Arctic team of the English Fisheries Laboratory consists of the following: M. Graham, G. C. Trout, A. J. Lee (Hydrographer), R. J. H. Beverton, J. Corlett, R. W. Blacker. Any of these may have been in charge of the cruises on the observations of which this paper is based. The paper is, however, due entirely to A. J. Lee, with suggestions from his colleagues.

Introduction.

The Barents Sea and the Bear Island—Spitsbergen fishing grounds together make a larger contribution than any other area to the landings of demersal fish in English ports. In 1947, for example, out of a total of 592,034 metric tons of demersal fish landed in England and Wales 218,478 metric tons, or 36.9 %, came from these areas, which rank first and third respectively in the table listing the principal fishing grounds in order of weight of landings (Table 1). The deep-sea trawlers that fish these rich Arctic grounds have become increasingly large in recent years and their fish holds have become correspondingly bigger, with the result that they are now becoming difficult to fill without extending the duration of the voyage to such a length that the fish caught first are liable to be stale when landed at the Humber ports of Grimsby and Hull.

The R. V. "Ernest Holt" was commissioned in December 1948 by the Ministry of Agriculture and Fisheries for work in Arctic waters and during the past two years she has been investigating the Bear Island fishery. The main objective of her work has been to find ways to speed up the catching of cod, the principal fish taken in the Bear Island area, and so to shorten the length of the voyages undertaken by commercial vessels and enable more fish to be landed in a fresher condition. A commercial voyage at present usually lasts for at least three weeks and a reduction of this length of time by four to six days is desirable, but the present level of landings must be maintained or increased.

The main line of research has been to find whether any relationship exists between the temperature of the bottom water and the abundance of cod. If such a relationship could be found, it might be possible to help commercial ships to fill their holds more quickly by recommending the use of a thermometer as a means of locating paying concentrations of fish in the Bear Island area.

Table 1. Total quantity of demersal fish landed in England and Wales from the principal fishing grounds by British vessels during 1947.

Fishing Grounds	Demersal fish landed (metric tons)
Barents Sea	126,756
North Sea	94,788
Bear Island and Spitsbergen	91,722
Iceland	63,276
Norwegian Coast	56,027
South of Ireland	34,133
West of Scotland	31,434
Faroe	26,441
Irish Sea	17,403
West of Ireland	10,138
English Channel	8,525
Rockall	5,556
Bristol Channel	3,153
West Greenland	91
Moroccan	1
Livers for which regions cannot be separately shown	22,590
Total...	592,034

Previous investigations in various regions.

Previous investigations into the relationship between cod and water temperature in various regions indicated that this might be a fruitful line of research. Much work has been done on the effect of temperature on spawning cod. For example, Beaugé (1932) states that cod can be found at a depth of 600 m. throughout the year all along the Norwegian continental slope and that during the spawning season they move into shallower water with temperatures between 2.5° and 5° C. and a salinity less than 35 ‰, but Eggvin (1933), in a more detailed study, concludes that during the Lofoten season the spawning cod are located in Vestfjord in a midwater transitional layer with a temperature between 3° and 6.5° C. In fact, Sund (1933) has detected dense shoals in this layer by means of an echo-sounder and Eggvin has since shown that it is possible to produce fishing forecasts based on the position and thickness of the layer. Taking examples from elsewhere, cod in the Skagerak have been shown by Dannevig (1933) to spawn in water of 4° to 6° C. and both Beaugé (1932) and Thompson (1943) think

that the Newfoundland cod mostly spawn in water between 3° and 5° C. There is therefore some measure of agreement between the various ranges of temperature given for spawning cod in different localities.

The cod taken at Bear Island are not in the act of spawning, however, and there has been but little previous work on the relationship between the abundance of this type of cod and temperature in any part of the Barents Sea. Maslov (1944), quoting Milinsky, states that the distribution of Russian catches in the central Barents Sea in 1934 and 1935 agreed well with the spreading of warm water towards the east and north-east and notes that the catches seemed to be related to the movement of the 2° C. isotherm, but he does not maintain that such an agreement will be obtained every year and thinks that the optimum temperature frequently lies between 1° and 2° C. Eggvin (1938), although giving no specific temperature range in which the cod may be found, regards the position of the mixing region of Atlantic and Arctic water on the East Finmark coast as determining the location of the coastal cod fishery which takes place in spring. When the Atlantic influence is strong the mixing region and the productive fishing areas are situated further to the eastward than when the Atlantic influx is weak.

When the results of researches on the relationship between the abundance of non-spawning cod and temperature in regions outside the Barents Sea are examined, it is found that the agreement on temperature ranges is not as great as in the case of spawning cod. In the Newfoundland region, le Danois (1924) states that cod seek water of between —2° and 6° C. and claims that hydrographical studies are important in order to determine the movements of the fish, but Thompson (1943) comes to the conclusion that the optimum temperature for large catches at Newfoundland varies according to locality and season. He states that a variation of 2° to 4° C. from the optimum temperature is sufficient to cause a scarcity of fish but that the total range of temperature within which cod have been found at Newfoundland extends from almost —2° to 12° C. It is doubtful whether the lower limits of temperature given by le Danois and Thompson are strictly correct. Dannevig (1930), as a result of a tank experiment, regards —1° C. as the critical temperature for cod and notes that in severe winters, when this temperature is found near the Norwegian Skagerak coast, dead cod are found in the outer skærgård. Furthermore, in another paper (1930a) he quotes Schmidt-Nielsen[1]) as having shown that the freezing point of the blood of some teleostean fishes lies between —0.5° and —1° C. The freezing point of the blood of cod has been determined experimentally by Dekhuyzen (1905) as being —0.73° C. when the freezing point of the water surrounding the fish is —1.73° C., and it seems probable, therefore, that the lower limit for cod should be about —1° C. Thompson also tabulates a series of "best" temperatures for cod, depending upon the locality, the season and the size of fish; for example, the "best" temperature range for large cod on the Newfoundland Banks is 0° to 3° C. in spring, and 3.5° to 5.5° C. in summer and autumn. Although Lumby (1951) has since shown that, on the basis of the data given in Thompson's paper, his evidence cannot be regarded as completely adequate, Thompson's paper reveals the complexity of the problem.

McKenzie (1934), working in the Nova Scotia area, is also aware of this complexity and states that in the Bay of Fundy and the inshore waters of the Atlantic coast of Nova Scotia excellent catches of cod can be taken over a wide range of temperature, from as low as —0.5° C. to as high as 15.5° C. Most fishing is carried on in water of 2° to 7° C. but this is possibly due to these temperatures being found more often than any others. He also examines by means of tank experiments the effect of temperature on the feeding habits of cod and finds that cod eat increasing amounts of food as the water temperature rises from 4.5° to 14° C., but that beyond this point the amount of food eaten decreases with increasing temperature. In addition, he shows that sudden increases of temperature can cause a decrease in the degree of feeding and thinks that in the sea off Nova Scotia such increases could cause a decrease in the size of the catch. Further, McKenzie and Hachey (1939) relate the hydrographical structure of the waters on the Scotian shelf to the annual catches of cod. They show that a cold intermediate layer with a temperature less than 5° C. comes into contact with the fishing grounds and acts as a deterrent to cod arriving there. The success of the fishery in a particular year is claimed to be related to the relative thickness, depth and degree of coldness of the layer in that year.

These researches in the Newfoundland and Nova Scotian areas, although establishing no simple relationship between cod abundance and temperature, gave rise to the afore-mentioned belief that a relationship might be found in the Bear Island area.

Conditions in the Bear Island area.

The fishing in this region has been shown by commercial vessels to be notoriously spotty. Prolific fishing with catches between 300 and 400 baskets (11 to 15 metric tons) per hour can be carried on at one point, whilst at the same time fishing at another point a few miles distant is giving only a few baskets per hour. (English Arctic fishermen report quantities caught in baskets. A basket contains 84 lbs. avoirdupois or approximately 38 kg.) Rapid changes of water temperature are also common in this area. The thermograph fitted aboard the R. V. "Ernest Holt" gives a continuous record of the surface temperature. Changes of temperature of 6° C. within a distance of half a mile have often been recorded during the past two years. No continuous record of temperature is avail-

[1]) Dannevig presumbly refers to Schmidt-Nielsen, S. & S., 1925. "Beiträge zur Kenntnis des osmotischen Druckes der Fische." K. Norske Vid. Selskab. Skr., 1923—4, Nr. 1. Trondhjem. 1925.

able for water close to the bottom, but spot bottom temperature observations taken at intervals of three or four miles have disclosed changes of temperature of 1.5° C. per mile. These rapid changes of both temperature and the abundance of fish strengthened the impression that a search for a relationship between the two might be profitable.

Collection of data.

In the field the original method of attack upon the problem was to proceed to an area in which commercial vessels were fishing profitably and then to make lines of trawl hauls in various directions through the paying concentration of fish, the paying level being taken arbitrarily as 40 baskets (1.5 metric tons) per hour. Bottom temperature observations were made immediately before and after each trawl haul. During later cruises this plan was often modified and, in order to test current hypotheses, hauls were purposely made in areas some distance from those in which the commercial vessels were operating. When commercial trawlers were absent from the Bear Island region or when fishing was slack, lines of trawl hauls were carried out in various localities around the island in order to test for the presence or absence of paying quantities of fish. Moreover, since the end of 1949 bottom and surface temperature surveys have been carried out in order to provide a more detailed picture than that given by the observations taken in conjunction with the trawl hauls.

Examination of the results collected during the past two years has shown that the above method of attack suffers from a disadvantage in that the results cannot be subjected to rigid statistical tests and it may be argued that the establishment of a permanent grid of hydrographical and trawling stations, which were to be worked every cruise, would have yielded results which could have been analysed more easily. On the other hand, it must be remembered that the weather in the Bear Island area is frequently very bad and, on this account, it is doubtful whether the whole of such a grid could have been worked during every cruise. The amount of available working time has been so small on some occasions that it has only been possible to make a few observations, and it has then been necessary to plan the cruise so as to obtain positive results only. This aim was more likely to be achieved if observations were made in vicinities where paying concentrations were known to exist.

The instrumental techniques employed have also suffered from various limitations. The bottom temperature observations have been made by means of a reversing frame, which contained two protected thermometers, and which was attached to a 4 mm. wire at a distance of 7 metres above a heavy terminal weight. The weight was lowered until it was felt to touch the bottom and the frame was operated by a messenger after the thermometers had been given sufficient time to take up the temperature of the water. Thus, the temperatures have been observed at a distance of 7 metres from the bottom whilst the trawl usually only sampled the 3 metres of water immediately above the sea-bed. It is thought that the temperature errors so incurred are small, however, as many full-scale hydrographical series using Nansen water bottles have been carried out in the area during the past two years and these show that the temperature gradient near the bottom is usually less than 0.02° C. per metre, although occasionally it reaches 0.05° C. per metre. Another drawback lies in the fact that, in view of the sharp temperature gradients which are known to exist in the Bear Island area, a continuous record of the bottom temperature during each trawl haul is really required. It has not been possible to devise an instrument capable of giving this, but the difficulty has been partly overcome by the introduction of bottom temperature surveys with only very short distances between the stations.

A Granton trawl with a 110 mm. mesh cod-end and a 68 ft. headline has been used throughout the work, apart from during the early cruises of 1949 when an 80 mm. mesh cod-end was used. The trawl, as a method of determining the distribution of fish present on the bottom, suffers from a disadvantage in that it is impossible to tell at what stage in a trawl haul the fish are actually caught and it is also possible that some are caught in midwater during the processes of shooting and hauling. In an area such as the Bear Island region, in which temperature and fish concentrations change rapidly, the reversing frame and the trawl cannot give an exact picture of the bottom temperature and the fish distributions respectively, and this must be borne in mind when the results of the past two years' work are examined.

Temperature limits for Bear Island cod.

The catch (in baskets) of cod per hour's fishing and the mean of the bottom temperature observations taken at the beginning and end of the haul were calculated for each haul, which has been made by the R. V. "Ernest Holt" during the past two years on the fishing grounds lying between latitudes 73° and 75° N. and west of the 21° E. meridian. The catch per hour was then plotted against the bottom temperature and it was found that paying catches have only twice been taken when the mean bottom temperature has been less than 1.75° C. Although it must be noted that fewer observations have been made in areas where such temperatures prevail (Fig. 1), it seems reasonable to regard 1.75° C. as the temperature limit below which good catches are rarely made. This limit only applies to the area west of the 21° E. meridian, however. East of this meridian paying catches have been taken during the summer months in temperatures as low as —0.3° C., but these fish differed from those caught west of longitude 21° E. in that they were feeding very heavily on capelan and krill, whilst those caught west of the meridian were either not feeding or feeding only lightly to moderately. It appears that in the area between the South—East Gully (Fig. 2) and Hope Island, cod will enter very cold water to feed, but to date the R. V. "Ernest Holt" has not

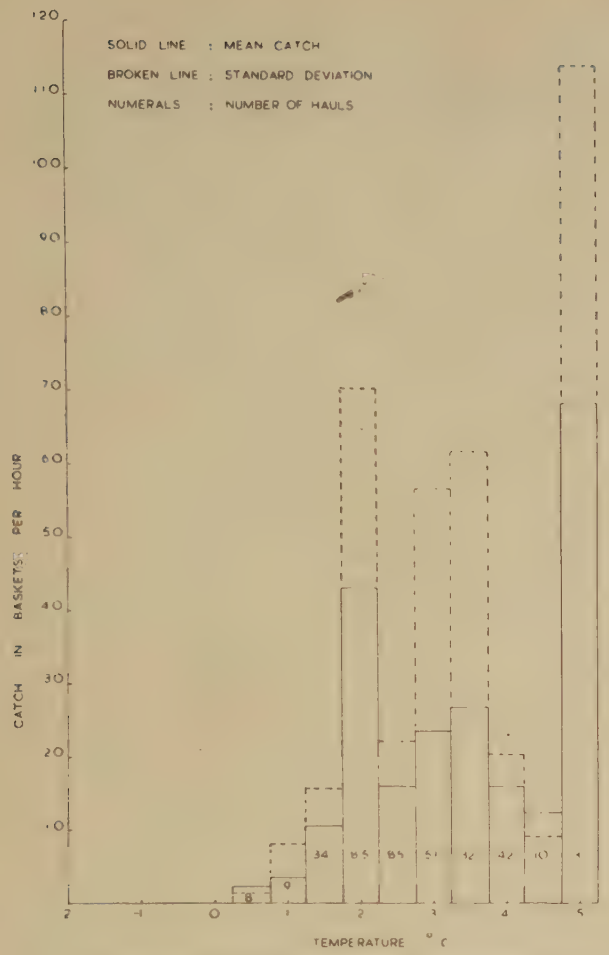


Fig. 1. Relationship between bottom temperature and mean catch of cod.

taken any fish in water with a temperature below —0.6° C.

It has been possible to evaluate the mean catch for various temperature ranges. In Figure 1 this has been done for successive 0.5° C. intervals of temperature, and it is seen that the mean catch exceeds the paying level of 40 baskets per hour in two temperature intervals, 1.75° to 2.25° C. and 4.75° to 5.25° C., but the latter can be ignored as the mean is only based on three hauls. If, however, the standard deviation of each mean is calculated, it is found to be nearly always greater than the mean itself and it is therefore useless to recommend any particular temperature range as being the most fruitful at all times.

The large standard deviations are due to the fact that both very high and very low catches have been taken in all temperatures above 1.75° C. This wide dispersion of the catches is partly due to the way in which the data have been collected and also to the fact that the temperature range, in which paying quantities of fish were found, varied on different cruises. At times no paying quantities of cod were taken at all, although large areas had a bottom temperature between 1.75° and 4.5° C.; and on cruises when paying quantities were found, the cod were not evenly distributed throughout the whole of the area that had a favourable bottom temperature. It is obvious, therefore, that other factors besides the hydrographical conditions must be taken into account in order to explain the distribution of cod at any one time. Biological factors, such as the migrations of the cod, the distribution of food and the distribution of benthos, must be taken into account and the hydrographical and biological patterns must be examined in conjunction with each other.

Hydrographical conditions: 1949—50.

There are two main types of water in the Bear Island area. Atlantic water is relatively warm and saline, and is brought to the region by the West Spitsbergen Current, which is the continuation of the Atlantic Current (Fig. 2). The latter enters the Norwegian Sea through the Faroe—Shetland Channel and the channel between the Faroes and Iceland, and runs along the length of the Norwegian coast before dividing just north of the Lofotens into the North Cape Current and the West Spitsbergen Current. The West Spitsbergen Current, which flows along the continental slope close to the westward of Bear Island, can therefore be regarded as one of the extremities of the Gulf Stream system. Arctic water originates in the North Polar Sea and the Siberian shelf seas to the north and east of Bear Island and flows in a south-westerly direction across the Bear Island—Spitsbergen Bank as the Bear Island Current (Fig. 2). It gives rise to a tongue of water of low salinity and low temperature around Bear Island. The two types of water meet in the Bear Island region, thus leading to the formation of a marked polar front south and west of the island.

Two hydrographical sections have been established in order to study the behaviour of these two main water masses in the western part of the Barents Sea. One section runs from Loppen in Norway to the southernmost point of Bear Island, Cape Bull; whilst the other runs along the 74°25′ N. parallel from Bear Island to longitude 13° W. The two sections were worked completely six times during 1949 and 1950 and the parts of the sections nearest to Bear Island were also worked on one additional occasion. The stations forming these two sections, which are known as the South and West Bear Island sections respectively, are shown in Figure 2.

The temperature-salinity relationships of the two types of water can be shown by plotting, as a T—S diagram, all the observations made at stations S (74°25′ N., 16°08′ E.) and M (74°08′ N., 19°14′ E.) during 1949 and 1950 (Fig. 3). Station S is situated in 520 fathoms in the West Spitsbergen Current, just off the shelf, whilst station M is in 45 fathoms on the Bear Island Bank and is in, or is close to, the Arctic water. If we regard Atlantic water as having a salinity above 35 ‰, it can be seen that the temperature of

Fig. 2. General current system of the western Barents Sea and the two standard hydrographical sections.

this water has ranged from 7.5° to 2.5° C. and that its salinity has not exceeded 35.17 ‰. Temperatures above 7° C. were recorded in the surface layers during the summer months only, a thermocline often being formed at this time. The temperature at 150 m. was usually between 4.6° and 5.6° C. and temperatures below 3° C. were not encountered until a depth of at least 450 m. was reached. Fishing at Bear Island rarely takes place below 400 m. depth. Figure 3 also shows that Atlantic water has always been found down to a depth of 600 m., but that it has not been found at a greater depth. Cruises made early in 1951, however, show that it can be found down to 800 m. The observations made below 600 m. at station S show the transition between the Atlantic water and the bottom water, which fills the Greenland and Norwegian Seas, and whose T—S relationship has been described by Nansen and Helland-Hansen (1909). It has a temperature between —1.1° and —1.2° C. and a salinity of 34.90 to 34.93 ‰.

The observations made at station M differ from those made at station S in that they are widely scat-

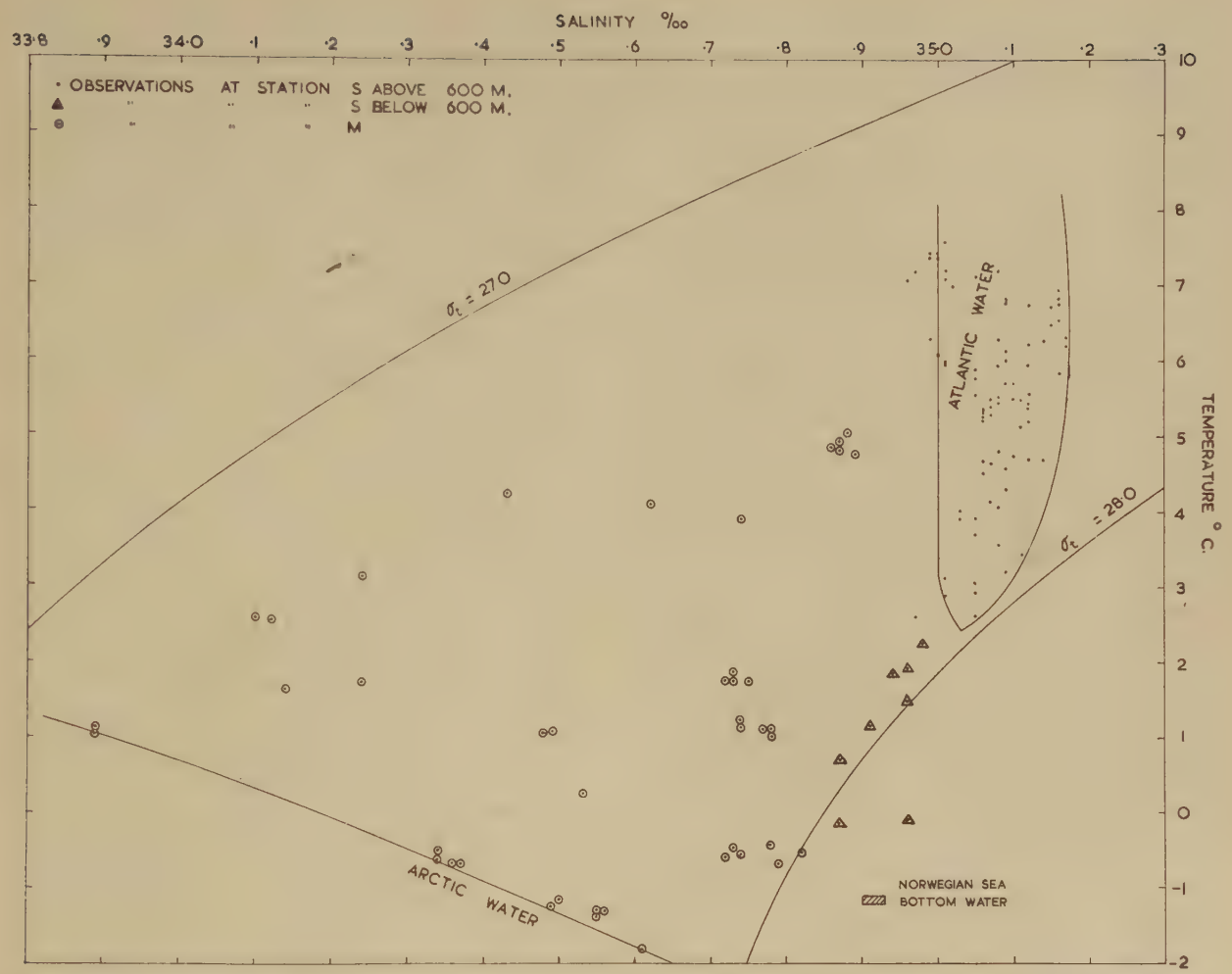

SALINITY ‰
33·8 ·9 34·0 ·1 ·2 ·3 ·4 ·5 ·6 ·7 ·8 ·9 35·0 ·1 ·2 ·3
OBSERVATIONS AT STATION S ABOVE 600 M.
" " " S BELOW 600 M.
" " " M
σt = 27·0
σt = 28·0
ATLANTIC WATER
ARCTIC WATER
NORWEGIAN SEA
BOTTOM WATER
TEMPERATURE °C.
10 9 8 7 6 5 4 3 2 1 0 -1 -2

Fig. 3. Temperature—salinity relationships in the Bear Island region.

tered on the T—S diagram. The temperature at station M has ranged from —1.8° to 5° C. and the salinity has varied between 33.9 and 34.9 ‰. A smooth curve can be drawn through the extreme observations and this can be regarded as defining the T—S relationship of the Arctic water. The temperature of the Arctic water has thus ranged from —1.8° to 1° C. and the other values of temperature and salinity for station M are seen to have been due to mixing between the Atlantic and Arctic waters.

The amount of water transported northwards by the West Spitsbergen Current has been found to fluctuate widely. It has been possible to calculate for seven cruises the average transport northwards across the West Bear Island section, between stations S and W (74°25′ N., 13°00′ W.) and above 400 m. depth. For this purpose the 750 dbar. surface has been used as the reference level. Table 2 shows the values obtained. The volume of water transported northwards is seen to have decreased from March 1949 until October 1949. The section was not worked fully again until March 1950 when the volume transported was once more small. It is unfortunate that, owing to trouble with the winches aboard the R. V. "Ernest Holt", samples could not be taken at a depth greater than 475 m. in March 1950. The 475 dbar. surface has therefore been used as the reference surface for the calculations for this month, and the value so obtained has

Table 2. Transport of water northwards across latitude 74°25′ N. between 13°00′ W. and 16°08′ W. and above 400 metres.

(Reference surface 750 dbars.)

Date	1949			1950			1951
	20-21 Mar.	12 Jul.	15-16 Sep.	20-21 Mar.	3-4 Jul.	4 Oct.	6 Feb.
Transport km.³/hr....	6.10	3.64	2.31	0.65[1])	5.00	1.05	12.21

[1]) 475 dbars. used as reference surface and a correction applied.

been multiplied by a correction factor based on a comparison of the values given when the 475 dbar. surface was used as the reference surface for other months with the values obtained when using the 750 dbar. surface for those months. The figure given for March 1950 is therefore only approximate but it is of the right order of magnitude. The amount of water transported northwards increased from this low value to a peak during the summer of 1950, only to decrease again in the autumn. It increased once more towards the end of 1950 and reached the highest value yet obtained in February 1951.

No transport values are available for the period between September 1949 and March 1950 but some stations along the West Bear Island section were worked in late November and the temperatures and salinities obtained suggest that there was an increased Atlantic influx during this period. The mean salinity of the whole water column has been calculated for all cruises for station Q (74°25′ N., 16°46′ E.), which is sited on the eastern edge of the West Spitsbergen Current, in 120 fathoms depth on the Bear Island Bank. The values obtained are shown in Figure 4 and it can be seen that the fluctuations of salinity have been identical with the fluctuations of water transport. It can also be seen that the mean salinity at station Q reached a maximum in November 1949—January 1950 and it is likely that the volume of water transported northwards also increased at this time.

The amount of Atlantic water transported into the Bear Island area has affected the bottom temperatures on the fishing grounds. When the Atlantic influx has been strong, temperatures have usually been high; and when the Atlantic influx has been weak and the Arctic influence strong, temperatures have been low. The temperature distribution on the fishing grounds has been also affected by the fact that the position of the axis of the West Spitsbergen Current varied with time and locality. The axis of the current was usually situated close to the continental slope but this was not the case along the whole length of the Bear Island Bank at any one time. The main part of the current often impinged upon the bank in one place, giving temperatures of 4° to 5° C. on the fishing grounds, and stood well away from it in another. Moreover, the current did not always strike the bank at the same place throughout the two years, except to the north-west of Bear Island where the North-West Gully furrows the shelf. Here bottom temperatures of over 4° C. were nearly always found. Further south, however, work on the West Bear Island section has shown that here the axis of the current was at times well away from the bank but that it was close to it on other occasions. In late March 1949, for example, it was 15 miles west of the continental slope, whereas in early June 1949 it was very close to the shelf. Counter-currents and eddies have also been found to have been formed on the eastern side of the West Spitsbergen Current along the boundary between the Atlantic and Arctic waters. These were transient features which complicated the bottom temperature distribution and slowly but continually changed the pattern of isotherms.

The North Cape Current is narrow and its strongest part is confined to the Norwegian coast, whilst the Bear Island Current is confined to the Bear Island Bank. Work on the South Bear Island section has shown that, in the area between these two currents, there has been a predominant movement of Atlantic water from the West Spitsbergen Current towards the east. The currents in this region have been weak and variable and a counter-current has often been found to the north of the North Cape Current, whilst eddies have been common along the front to the south of Bear Island. The temperature distribution of the bottom water on the slope forming the southern edge of the Bear Island Bank has depended upon these eddies and the amount of Atlantic water brought to the slope. The temperature has normally been between 1° and 2.25° C., with occasional temperatures of less than 1° C. at depths greater than 450 m. in the Bear Island Channel, but, with the exception of March 1949, temperatures have increased when the volume of Atlantic water transported by the West Spitsbergen Current has been high. Thus, in 1950, in January and again in November to December, a band with a temperature above 3° C. was found south of Bear Island, whilst in October temperatures above 5°C. occurred. These latter were in shallow water and probably represented the culmination of the summer influx of Atlantic water. A temperature maximum was found at 75 m. at many points around the island during this month, but it was only found to be in contact with the bottom in the area to the south of Cape Bull.

The axis of the Bear Island Current also shifted its position from time to time. Sometimes the tongue of water giving bottom temperatures between —1.8° and 1° C. encircled Bear Island. On other occasions it was to be found either to the north or south of the island. In 1950 it reached its maximum southwestwards extension in the months February to April, but no information is available to establish

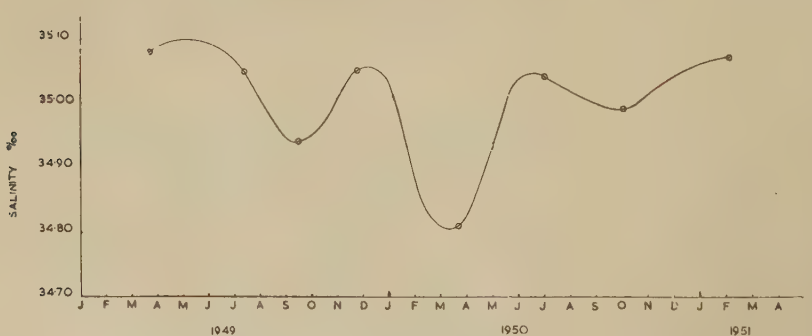


Fig. 4. Mean salinity at Station Q (74° 25′ N., 16° 46′ E.).

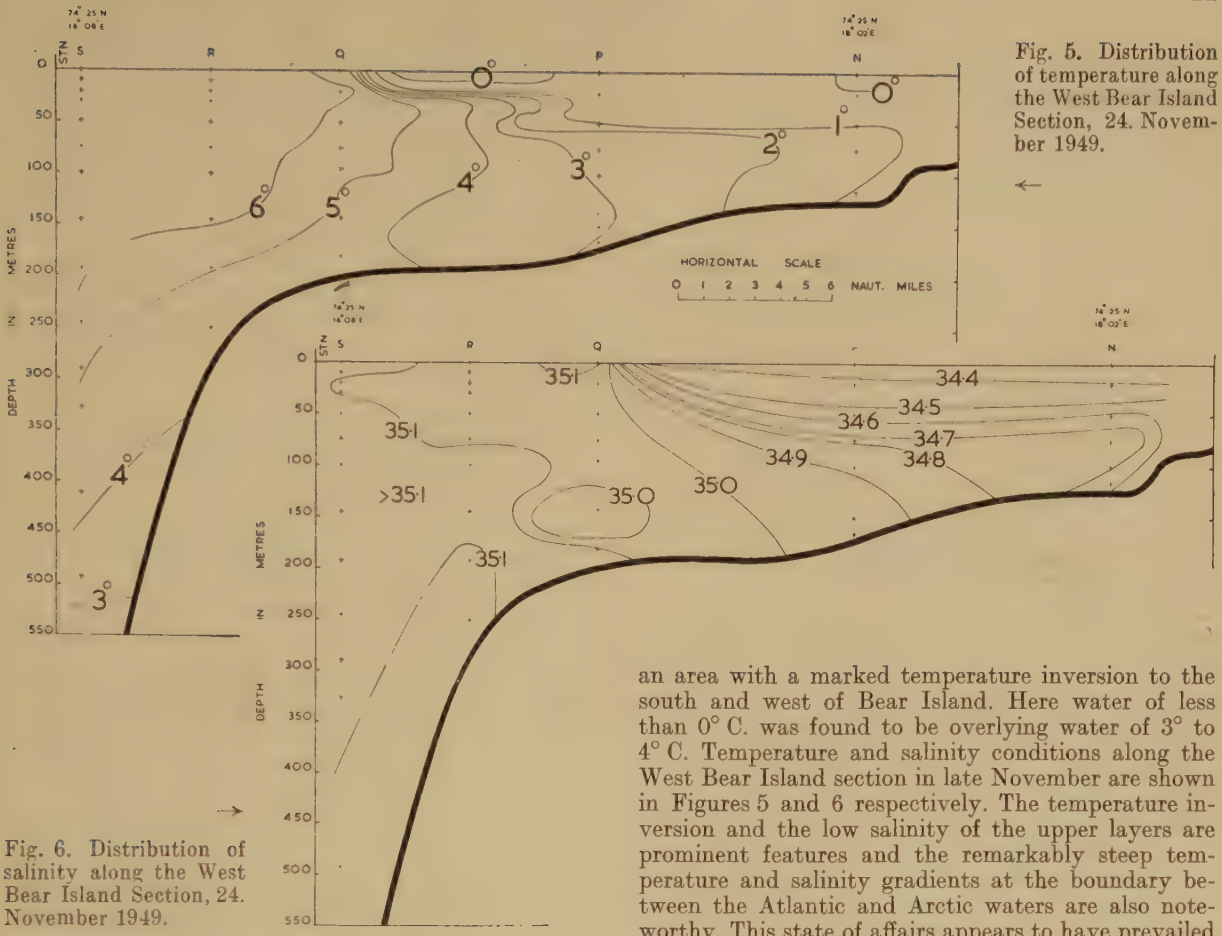


Fig. 5. Distribution of temperature along the West Bear Island Section, 24. November 1949.

Fig. 6. Distribution of salinity along the West Bear Island Section, 24. November 1949.

whether this was also the case in 1949. After April it slowly withdrew to the north-east so that by August it was displaced to the east and north-east of Bear Island. In 1950 it did not start to advance again until November, but in 1949 it pushed south-westwards a month earlier and by late November was close to the position it occupied in February 1950.

This south-westerly movement of the Arctic water in 1949 was first noticeable in the surface layers in September and became pronounced in October. It appears to have been greatly assisted by the north-easterly winds which prevailed in the latter month. Table 3 shows the monthly residual winds at Bear Island for 1949 and 1950. These have been obtained by extracting the values of wind force and direction given for each day in the Daily Weather Report of the British Meteorological Office and calculating their resultant. From Table 3 it will be seen that the residual wind in October 1949 had a speed of 10.6 m.p.h. and a direction of N. 58° E. and this undoubtedly accounts for the strong advance of the upper layers of the Arctic water in this month. Surface water of low salinity and temperature moved especially far south-westwards over the denser Atlantic water, giving rise to an area with a marked temperature inversion to the south and west of Bear Island. Here water of less than 0° C. was found to be overlying water of 3° to 4° C. Temperature and salinity conditions along the West Bear Island section in late November are shown in Figures 5 and 6 respectively. The temperature inversion and the low salinity of the upper layers are prominent features and the remarkably steep temperature and salinity gradients at the boundary between the Atlantic and Arctic waters are also noteworthy. This state of affairs appears to have prevailed with only slight modification until January 1950 when the area covered by the inversion began to decrease. A section worked to the south-east of Bear Island in this month showed that the cold, low salinity, surface layer was breaking up at its edges.

In contrast, it can be seen from Table 3 that, although the residual wind in September had been easterly, the residual wind in October 1950 was southerly and did not become north-easterly until December in that year. This resulted in the south-westerly

Table 3. Monthly residual winds: Bear Island.

Month	1949		1950	
	Direction	M.P.H.	Direction	M.P.H.
Jan.	N. 56° E.	8.9	N. 86° E.	2.0
Feb.	S. 41° E.	6.2	N. 53° E.	11.8
Mar.	S. 44° E.	6.9	N. 32° E.	3.3
Apr.	N. 83° E.	7.8	N. 82° E.	5.9
May	N. 57° E.	16.4	N. 03° W.	5.8
Jun.	N. 80° E.	5.1	N. 61° E.	4.6
Jul.	N. 59° W.	5.3	N. 36° E.	1.7
Aug.	S. 23° E.	4.3	S. 35° E.	3.9
Sep.	S. 80° W.	3.9	N. 80° E.	11.0
Oct.	N. 58° E.	10.6	S. 07° W.	4.3
Nov.	S. 50° E.	8.5	S. 76° E.	6.7
Dec.	S. 69° E.	12.9	N. 42° E.	11.2

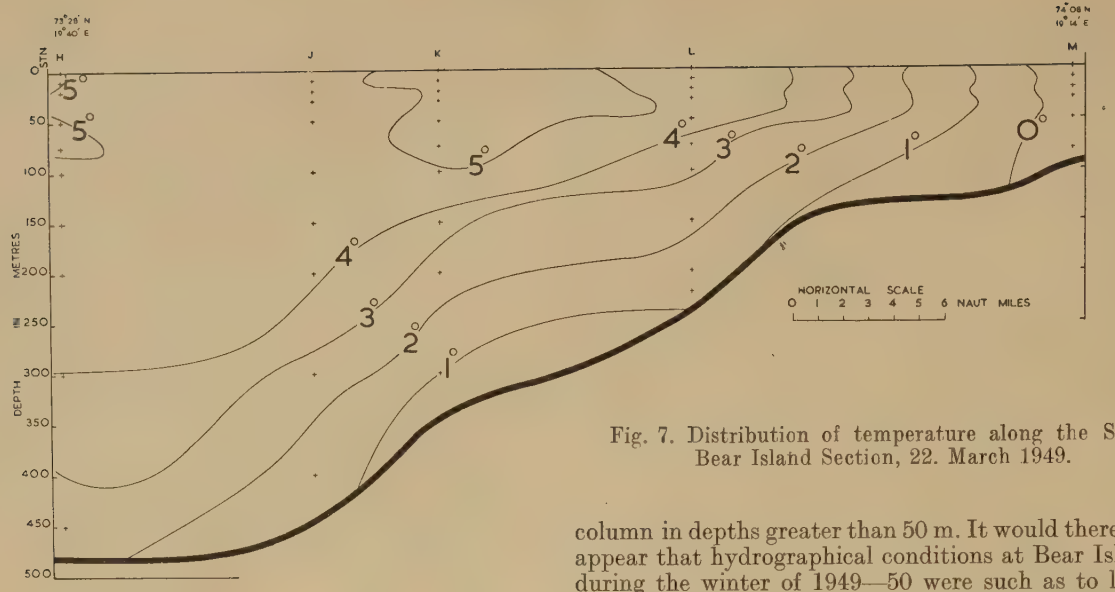


Fig. 7. Distribution of temperature along the South Bear Island Section, 22. March 1949.

advance of the Arctic water being later in 1950, and a well-marked temperature inversion was not established by the end of November. Two other factors also assisted in delaying the formation of the inversion in 1950. Firstly, the summer influx of Atlantic water was stronger in 1950 than in 1949 and the south-western boundary of the Arctic water was therefore pushed further to the north-east. This delayed the formation of the temperature inversion to the south and west of Bear Island later in the year, as the Arctic water had to travel over a greater distance across the shelf in order to reach that area. Secondly, the mean air temperatures for October and November were higher in 1950 than in 1949, and this retarded the cooling of the water on the shelf.

The advance of the Arctic water which started in autumn 1949 culminated in the formation of young ice around Bear Island in February and March 1950. In high latitudes when water of low salinity overlies water of higher salinity it is possible for the winter cooling from the atmosphere to be confined to the upper layers only. Thus, water of salinity 34.6 $^0/_{00}$ will still be less dense, even when cooled to nearly freezing point, than water of salinity 35 $^0/_{00}$ with a temperature of 3° C., and, if the former overlies the latter, convectional mixing due to cooling will be greatly reduced. Moreover, the thickness of the homogeneous wind-stirred layer is proportional to the wind strength and to the cosecant of the latitude, according to Rossby and Montgomery (1935), and is therefore small in high latitudes. Although the mean wind speed at Bear Island during the period between November 1949 and February 1950 was 18 m.p.h., the homogeneous wind-stirred layer would not exceed 40 m. in depth. The amount of mixing that can be caused by the strong tidal streams, which flow across the Bear Island Bank, is not yet known, but it does not seem to be sufficient to produce a homogeneous water column in depths greater than 50 m. It would therefore appear that hydrographical conditions at Bear Island during the winter of 1949—50 were such as to limit cooling to the upper layers and thus encourage ice to form, whilst bottom temperatures remained relatively high.

No observations are available for the winter of 1948—49, but a comparison of the sections worked at the end of March 1949 with those worked at the same time in 1950 shows a significant difference. Figures 7 and 8 show conditions on the South Bear Island section in March 1949 and 1950 respectively. It will be observed that in 1949 nearly the whole of the bottom between stations L and H was covered by water between 0° and 2° C., whilst in 1950 the temperature of the bottom between stations L and H was always above 2° C. Similarly on the West Bear Island section, bottom temperatures in 1949 were between 1° and 3° C., whereas in 1950 they were between 1° and 4° C. These temperature values are contrary to those that might have been deduced from a study of the amount of Atlantic water entering the area, for transport by the West Spitsbergen Current was high in March 1949 and very low in March 1950. This reversal may be partly accounted for by the fact that in March 1949 on the West Bear Island section the axis of the West Spitsbergen Current was well away from the continental slope, but the structure of the water on the Bear Island Bank must also be considered.

It is thought that in the first months of 1949 the bank was covered mainly by Atlantic water because in March the salinity everywhere was high, exceeding 34.9 $^0/_{00}$ at all stations with the exception of M. At station Q the mean salinity was 35.08 $^0/_{00}$, its maximum value during the past two years (Fig. 4). The low salinity surface layer characteristic of the succeeding winter was completely absent, probably because the wind conditions were unfavourable, the residual winds in February and March being south-easterly. Hydrographical conditions on the Bear Island Bank in early 1949 appear, therefore, to have been favourable

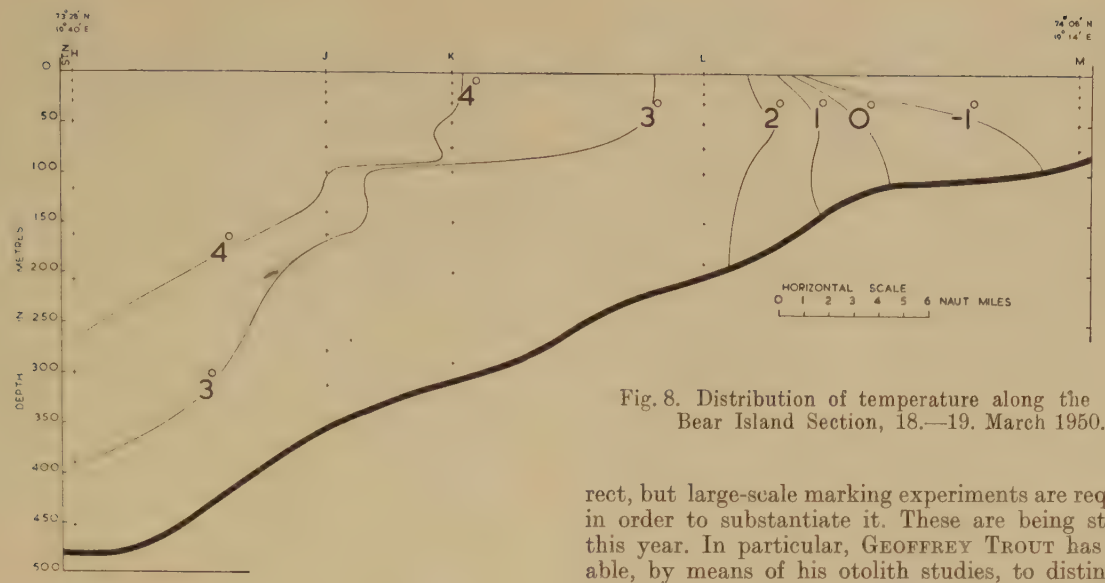


Fig. 8. Distribution of temperature along the South Bear Island Section, 18.—19. March 1950.

to the establishment of a vertical winter circulation, allowing the water at all depths to be cooled and become heavy. A study of the distribution of density at this time indicates that the water was sufficiently cooled for "cascading" over the continental slope, similar to that described by Cooper and Vaux (1949) from the Celtic Sea, to occur. The water on the bank became sufficiently heavy to flow to the edge of the shelf and run down the continental slope, thus causing the bottom temperatures on the fishing grounds to be lower than in March 1950, although the Atlantic influx was then weaker.

It should also be noted that the salinity of the water on the bank was much higher in March 1949 than in March 1950 (Fig. 4), and that "cascading" is more likely to occur when the salinity of this water is high, as it will require less cooling than when the salinity is low in order to make it heavy enough to flow down the continental slope. Thus in 1950, although there were some areas in which the water column was homogeneous, the possibility of "cascading" occurring there was reduced.

Biological factors.

The migration of mature cod from the Bear Island—Spitsbergen Bank to the Lofoten area to spawn has long been known. Less is known of the migrations of the immature cod, however. Maslov (1944) has described a migration pattern based largely on the activities of British trawlers in the Bear Island area. His scheme of migrations is given in Figure 9, which shows the immature cod as making similar migrations to the mature cod as far as the Bear Island—Hope Island—Spitsbergen area is concerned, but wintering south of Bear Island instead of going to the Lofotens. Our own researches during the past two years have tended to show that Maslov's hypothesis may be mainly correct, but large-scale marking experiments are required in order to substantiate it. These are being started this year. In particular, Geoffrey Trout has been able, by means of his otolith studies, to distinguish two populations of immature fish. He has formed the hypothesis that these populations mix in the Bear Island area, particularly from December to March. Separation occurs in April to May, one population moving north-eastwards towards Hope Island which is reached in September. This group enters very cold water to feed on capelan en route to Hope Island and it returns to Bear Island in November. The movements of the second population is thought to be to and from the Spitsbergen area. It is not known whether the immature cod do actually winter just south of Bear Island, as shown by Maslov, or whether they use this region as a gathering ground before moving to an area further south. This question is also being examined by means of experiments this year.

It has not yet been possible to evaluate exactly

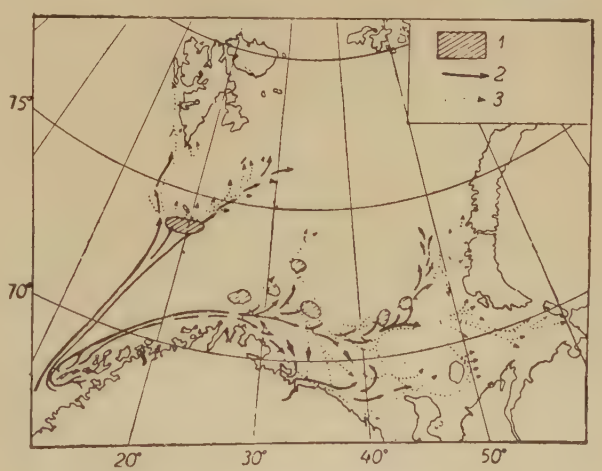


Fig. 9. Maslov's scheme of migrations of the cod.

1. Wintering grounds of immature cod.
2. Migrations of mature cod.
3. Migrations of immature cod.

the importance of food as a factor influencing the distribution of cod in the Bear Island area. The fish caught in the region west and south of the island have never been feeding more than moderately and their food has varied both with time and place. In July 1950, for example, the main food was *Limacina helicina*, whilst later in October it consisted mainly of young herring. At various other times it has consisted of euphausids, shrimps, brittle stars, *Beroë*, Hyperiid amphipods, *Pandalus borealis*, *Clione*, *Hyas araneus* and fish. The small amount of food found in the cod's stomachs and the wide variety of food eaten have given the impression that the fish were not actively hunting for food, like the cod which pursue the capelan towards Hope Island in the summer, but that they were taking whatever came to them. If this was the case, it is likely that the distribution of food did not greatly influence the distribution of the cod, but the statement by Brotsky (1931) that the cod in the Barents Sea form dense shoals when food is scarce and disperse on arriving in a region where it is abundant must be borne in mind.

The influence on the cod of the types of bottom and of the benthos found in the area has also not been examined completely, but it has been observed that cod were not taken where certain sponges and *Alcyonidium* were found in quantity.

It has been suggested that the cod are found in certain depths at certain seasons, but although the fish have been observed to move from deep water in winter to shallow water in summer, they have been found on many occasions to be in a wide range of depths. For example, in January 1950 paying quantities of cod were taken to the south of Bear Island in depths ranging from 60 to 150 fathoms. Furthermore, they have not been taken in the same depths at corresponding times in different years. In November 1949 the heaviest catches taken south of the island were in 115 fathoms whilst in November 1950 they were taken in 60 fathoms. Although it must be remembered that more than one population of fish is involved, it seems that depth does not exert a direct influence on the distribution of the cod.

Preparation of charts showing bottom temperature and fish distributions.

All the above biological and hydrographical factors must be borne in mind when examining the charts showing the distributions of fish and bottom temperature (Figs. 10—22). It must also be remembered that the maximum area considered measures only 120 by 75 miles. The charts were constructed by superimposing "catch contours" on the bottom isotherms. The observations of bottom temperature made during a cruise have been regarded as being simultaneous, except in November 1950 when a cruise of long duration was carried out. Two separate charts have been prepared for this cruise. The observations forming the basis of each bottom temperature chart were actually made over periods of up to eleven days, but the changes that take place at Bear Island during periods of this length are not great and each chart can be regarded as being representative of the bottom temperature conditions over the period concerned.

The "catch contours" have been obtained by calculating the catch in baskets per hour for each haul and assuming that this was the rate of fishing at the midpoint of the haul. When hauls were of more or less than one hour's duration, the catch per hour was calculated by assuming that the catch varied directly as the duration of the haul. The isopleths were then drawn in the usual way. It will be noted that the contours are thus based on two assumptions but it is felt that they are the best that could be made in the circumstances. It would have been sounder if it had been possible to express the catch in terms of distance, but, although the positions of shooting and hauling are known, the nature of these operations make it difficult to determine the actual distance traversed by the trawl along the sea-bed. Experiments are now being made with a device incorporated in one of the bobbins in order to obtain this distance. Furthermore, the charts in their present form are more useful to commercial vessels, as these ships are only interested in the catch per hour.

The conception of "catch contours" is open to three main objections. Firstly, a certain amount of personal bias can be said to enter into the drawing of the isopleths. This objection applies to all contour drawing, but the bias has been reduced to a minimum by drawing the "catch contour" chart independently of the bottom temperature chart and then superimposing one upon the other.

The second objection can be based on the grounds that the hauls are not made simultaneously and that the time factor is ignored. This objection cannot be avoided and is more serious than in the case of the bottom temperature isotherms. The fish may be moving on account of biological factors and they are situated in water which is also being moved, mainly by the tidal streams. Little is known about these streams in the Bear Island area but they appear to flow along the isobaths. They do not seem to affect the bottom temperature distribution, except perhaps in minor details, but it is possible for them to move a passive shoal of fish over short distances to and fro along the shelf. It must be remembered, therefore, that when more than one concentration of fish is shown on a chart the same fish may be included in each concentration. Nevertheless, the chart will still at all times show the relationship between the fish distribution and the bottom isotherms, whether the fish distribution can be regarded as simultaneous or not, and therefore the chart will not lose its value.

Finally, the variability in catch in replicate hauls has not been examined. Hauls have been repeated in the same place after periods of a few days and the significance of the time factor involved has been discussed above, but they have not been made at very short intervals of about an hour in order to see if the variability in catch is such that the contours will have statistical significance. Elsewhere Barnes and Bage-

NAL (1951) have examined the variability in catches obtained by short repeated hauls with a standard 54ft. headline, V.D. trawl over an inshore ground and find that, using logarithmic values, the coefficient of variation ranges from 40 to 85 %, including both round and flat fish. Taking 75 % as a representative value for the coefficient and converting to actual catches, they find that the fiducial limits would be 30—300 % for a single observation from a single haul of half an hour duration. The catches of a given species from two separate hauls could not, on this basis, be considered to be significantly different unless one was less than a third of the other.

From this example it can be seen that the catches in repeated hauls can have a high coefficient of variation and this must be borne in mind when attempting to contour fish populations. Although no data are available for estimating the variability of catches in the Bear Island area, our experience during the past two years seems to show that it is not as high as that found by BARNES and BAGENAL in the Clyde. Definite trends in the size of catch have been found when carrying out lines of trawl hauls and these would have been masked had the variability been great. It has also been found to be possible to contour the catches using small intervals and yet obtain good agreement between the isopleths for all sizes of catch, from those exceeding 100 baskets down to those below 10 baskets. A high variability of catch is unlikely to have allowed this to be done. It so happens that the values of the contours selected, 15, 40 and 120 baskets per hour, are almost significantly different on the statistical basis given in the paper by BARNES and BAGENAL, although they were originally chosen on account of their commercial significance before this paper became available. The contours for each cruise are shown in Figures 10—22. Hauls outside the shaded areas yielded less than 15 baskets per hour.

The Relationship between the Bottom Temperature and Fish Distributions in Particular Months.

April-May.

The temperature and fish distributions in the Bear Island region were first examined by the R.V. "Ernest Holt" from 26. April to 4. May 1949 (Fig. 10). The work was confined nearly wholly to the area south-west of the island, where two lines of trawl hauls were carried out at approximately right angles to each other through a group of trawlers. Figure 10 shows that catches of cod of over 15 baskets per hour were taken in an elliptical-shaped area, which was located in water of 2° to 3° C. In the centre of this area catches of over 40 baskets per hour were taken, but the reports obtained from commercial vessels indicated that they were taking much higher catches than this in the same area, although the fishing was spotty. Hauls in the very warm water to the south of latitude 73° N. yielded few cod and the main concentration of fish seems to have been in about 210 fathoms depth at the foot of the Bear Island Bank. The line of hauls running across the bank in a south-south-westerly direction from Bear Island gave hardly any cod at all until water of over 2° C. was reached in 200 fathoms depth. It would seem that the fish were avoiding water of less than 2° C. and that they had been driven to this depth by the fact that most of the Bear Island Bank was covered by cold water, whose origin and "cascading" to great depths have been described above. If so, the hydrography may be said to have influenced the fish distribution on this occasion.

Some fish were also taken in water of about 1° C. in the North-West Gully but these differed from those taken farther south in that they were feeding heavily on krill, whilst those taken in water of over 2° C. south of the island were feeding only slightly. The few cod, which were taken on the bank south of the island in temperatures of less than 2° C., were also feeding heavily on krill. The fish in water below 2° C. were therefore behaving differently from those in water above 2° C., but no information is available in order to determine whether this difference in behaviour was related to the distribution of krill at that time.

Temperature conditions in 1949 can be contrasted with those prevailing at the same time in 1950 (Fig. 11) when the 2° C. isotherm is seen to have been located in much shallower water south of the island, the hydrographical structure during the winter of 1949—50 having prevented the "cascading" of cold water down the slope. Only a few trawl hauls were made in the Bear Island area in 1950 and these did not reveal any quantity of fish. Reports from commercial vessels also show that there were no paying fish concentrations anywhere in the vicinity of the island. The wider area covered by warm bottom water may have encouraged dispersal of the fish.

The R. V. "Ernest Holt" made a number of hauls in the area between 90 and 110 miles east of the island and found paying quantities of fish in bottom temperatures between 2° and 3° C. in 160 to 170 fathoms. A number of commercial trawlers were getting good catches in this area and the fish were found to be feeding heavily on capelan. TROUT's otolith studies show that these fish formed part of the population that moves towards Hope Island in the summer and it is noteworthy that similar fish were caught in this area, but in shallower water, in July 1949. As no hauls were made in this eastern area in April—May 1949, it is a matter for conjecture as to whether the north-eastward migration started earlier in 1950 than in 1949. The wider area covered by water of over 2° C. in April—May 1950 might be said to have allowed the fish to move earlier to the east in that year compared with 1949, but against this must be set the fact that the population, which migrates between Bear Island and Hope Island, enters very cold water to feed and

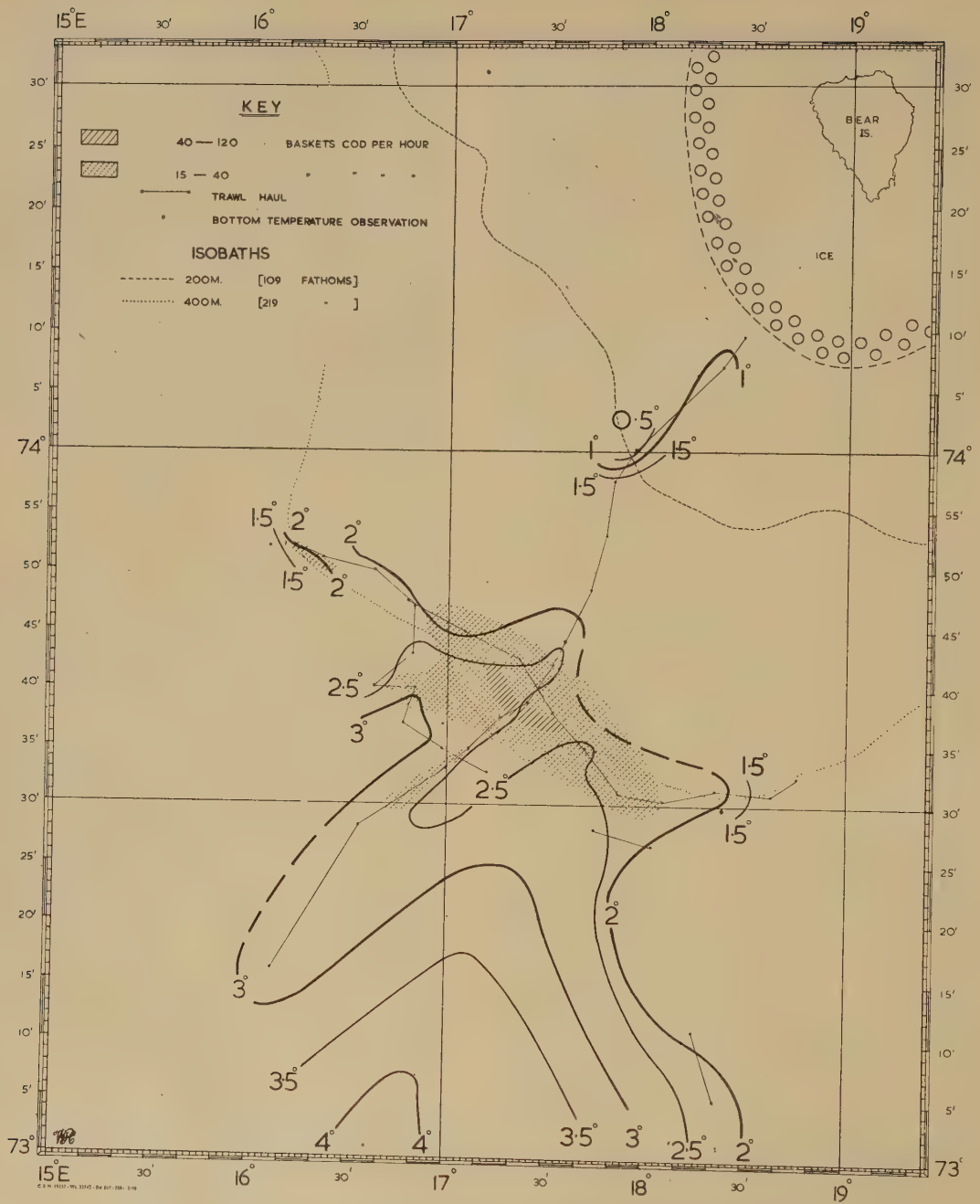


Fig. 10. Distributions of fish and bottom temperature in the Bear Island area, 26. April—4. May 1949.

it is difficult to see why the cold water, which covered all the southern flanks of the Bear Island Shelf in April—May 1949, should have acted as a barrier to these fish at this time.

(Cruises carried out during May and June 1951 show that the hydrographical conditions in this eastern region were similar to those prevailing in 1949. "Cascading" had occurred and bottom temperatures were below 2° C. Although many hauls were made over a wide area, catches were always less than 5 baskets per hour. The cod were again found to be feeding on capelan. These results give some support to the supposition that the higher bottom temperatures found in 1950 allowed the cod to move eastwards earlier in that year.)

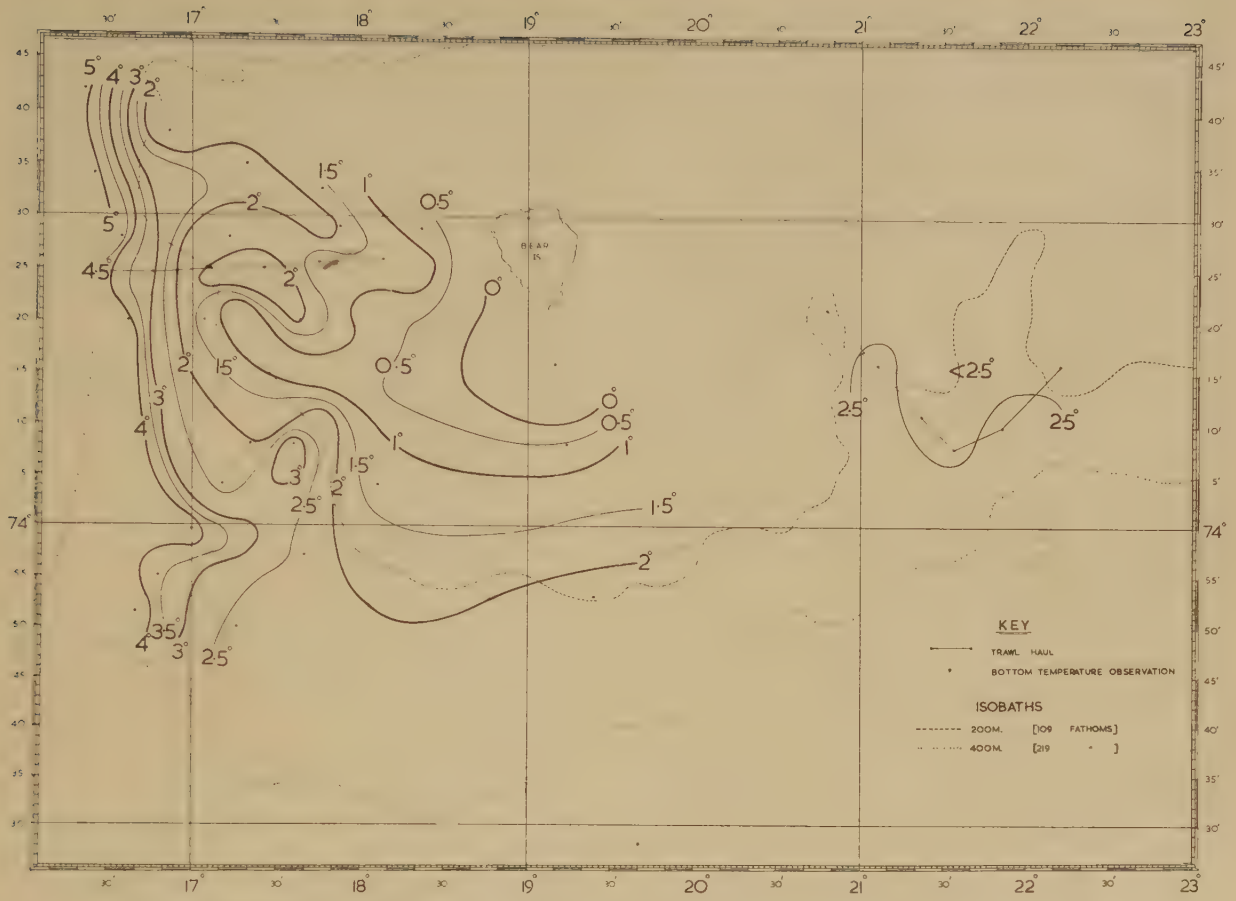


Fig. 11. Distribution of bottom temperature in the Bear Island area, 26. April—5. May 1950.

May-June.

When the R. V. "Ernest Holt" left Bear Island at the beginning of May 1949, wireless reports indicated that commercial ships were getting good fishing to the west of the island. Figure 12 shows conditions in this area when she returned at the end of the month. Bottom temperatures above 2° C. were confined to a long narrow strip along the edge of the shelf with a tongue entering the North-West Gully. In this strip temperatures up to nearly 5° C. were found. The cold water, which covered the bank in March and April, was still present and was the main reason why the area covered by warm water was small and was bounded by sharp temperature gradients on its eastern side. The sharp gradients on its western side are due to the fact that the continental slope here is very steep, so that the Norwegian Sea Bottom Water is quickly encountered on leaving the shelf. The sharp gradient on the western side of the Atlantic water is, therefore, always a permanent feature of the bottom temperature pattern.

The concentrations of cod were in depths between 90 and 160 fathoms and are seen to have been confined to the narrow strip where the Atlantic water touched the bank. Extremely high catches of up to 300 baskets per hour were taken by the R. V. "Ernest Holt" and commercial vessels enjoyed equally successful fishing until at least mid-June. The western boundary of the paying area is well-established and its eastern boundary is clearly defined in the extreme south. In the north, however, no hauls were made in shallow water and it is impossible to fix the eastern 40 basket per hour contour in this region. The paying catches were taken in bottom temperatures ranging from 1.5° to nearly 5° C., but as no hauls were made in temperatures of less than 1.5° C., this lower temperature limit cannot be regarded as definite. The fish in general were not feeding and many had empty stomachs, although two hauls in water of less than 2° C. south-south-west of Bear Island consisted of fish feeding heavily on krill.

Shoals of fish were detected over wide areas by the echo-sounder, especially in the region north of latitude 74°30′ N. They were off the bottom at depths between 70 and 120 fathoms. Temperature observations were frequently made in these shoals which were found to be in water between 3.5° and 5.3° C. Some salinity

samples were also taken and these show that the shoals were always in Atlantic water. It is possible that in some hauls fish were taken in the warmer midwater and not in the colder bottom water. If this was so, the range of temperature in which the fish were located would, therefore, be less than that indicated by the bottom temperatures.

Norwegian investigations carried out in the region in early June 1949 give some additional information. Rasmussen (1949) finds that the continental slope had temperatures above 3° C. in the depths usually fished by liners. He shows that temperatures were below 3° C. in 1946—48 and that the commercial fishery in these years was not as satisfactory as in 1949 and 1938 when temperatures over 3° C. were found. His sections show the hydrographical structure in the various years and that for 1949 is reproduced in Figure 12.

Conditions in 1950 were somewhat similar to those in 1949 (Fig. 13), but the area of bottom covered by water with a temperature over 2° C. was much greater; 1,170 square miles as compared with 580 square miles in 1949. The area covered by water over 4° C. was less than in 1949 and the maximum bottom temperature recorded was also lower, probably owing to the fact that the volume of Atlantic water being transported into the area was slightly less than in 1949; but the differences in the temperature gradients and positions of the 2° C. isotherm for the two years are due to the differing hydrographical conditions in the respective preceding winters, the smaller area covered by water below 2° C. in May 1950 being due to the absence of vertical mixing and "cascading" earlier in the year.

Catches of cod were again heavy and were taken mainly in 145 to 170 fathoms, but they do not seem to have reached the same high level as in 1949. This was probably due to the fact that the cod were no longer restricted to a narrow band of high temperature and were able to disperse over a wider area. Echo-sounder traces were observed and these also indicate that the fish were not as concentrated as in 1949, since on this occasion they were observed only at scattered points and not over large areas. There is also evidence that some of the traces may have been due to *Sebastes*. The fish were feeding lightly, the main food being euphausids, and it is not thought that this affected their distribution.

Figure 13 shows that a tongue of warm water was pushing eastwards along the bottom in latitude 74° 20′ N. and that it was bordered to the north and south by colder water moving westward, the more pronounced cold tongue being to the south. A vertical section was worked in this area and from this it has been found that these tongues were most pronounced in the lower layers.

The "catch contours" show that the fish were taken mainly in temperatures between 2.5° and 4° C. and that on the edge of the shelf there were two areas of heavy fishing, in which catches of over 120 baskets per hour were taken. It is noticeable that these two areas were separated by the southern tongue of cooler water. It is considered to be unlikely that the same fish were sampled in each area. Commercial vessels were getting good fishing in the southern area on 27.—28. May and in the northern area from 29. May to 4. June. The R. V. "Ernest Holt" sampled both groups on 29. May and the southern group again on 30. May, whilst the intervening area of low catches was sampled on 30. May. The fish may have been moved about by the tidal streams in the area. Little is known about these, but, using the information that is available, it is impossible to account for the cod distribution as being due to only one group of fish.

If the cod are assumed to have been brought to the shelf by Atlantic water and to have been part of a large population to the west of the shelf, the distribution can be explained, as the intervening cool tongue was primarily of Arctic origin and would contain less fish. Some support is added to this hypothesis by the fact that a third paying concentration of fish on the southern edge of the North-West Gully was in shallower water, 100 fathoms compared with 145—170 fathoms for the fish further south, and it was in this northern area that the West Spitsbergen Current made its most eastern encroachment on to the Bear Island Bank. On the other hand, it will be noted that not all the area covered by Atlantic water yielded paying fish.

Finally, when Figure 13 is compared with Figure 11, it is seen that, although the area covered by warm water increased during May in accordance with the increasing Atlantic influx, Atlantic water was already impinging on the shelf in early May, when hauls in the position, which gave paying quantities later in the month, yielded no fish. Thus, although the distribution of bottom temperature was favourable over a long period, paying catches of fish were not taken throughout the period, presumably because the fish were migratory and had not reached the area in early May.

June-July.

Figure 14 shows the temperature distribution from 29. June to 7. July 1950. The area covered by water above 2° C. had further increased as the Atlantic influx approached its climax. Unfortunately, it was impossible for the R. V. "Ernest Holt" to do any trawling during this cruise and information about the distribution of the cod had to be obtained from commercial vessels. These fished at first in 60 to 90 fathoms to the south and south-west of Cape Bull, but later they moved to the north-west of the island and obtained good catches in 70 to 130 fathoms along the southern edge of the North-West Gully, the bottom temperatures in both areas being between 2° and 3° C. The heavy fishing in deep water to the west of the island seems to have come to an end before this cruise, although Atlantic water was still in contact with the bank. The fish taken by the commercial vessels were reported to be feeding lightly on *Limacina*

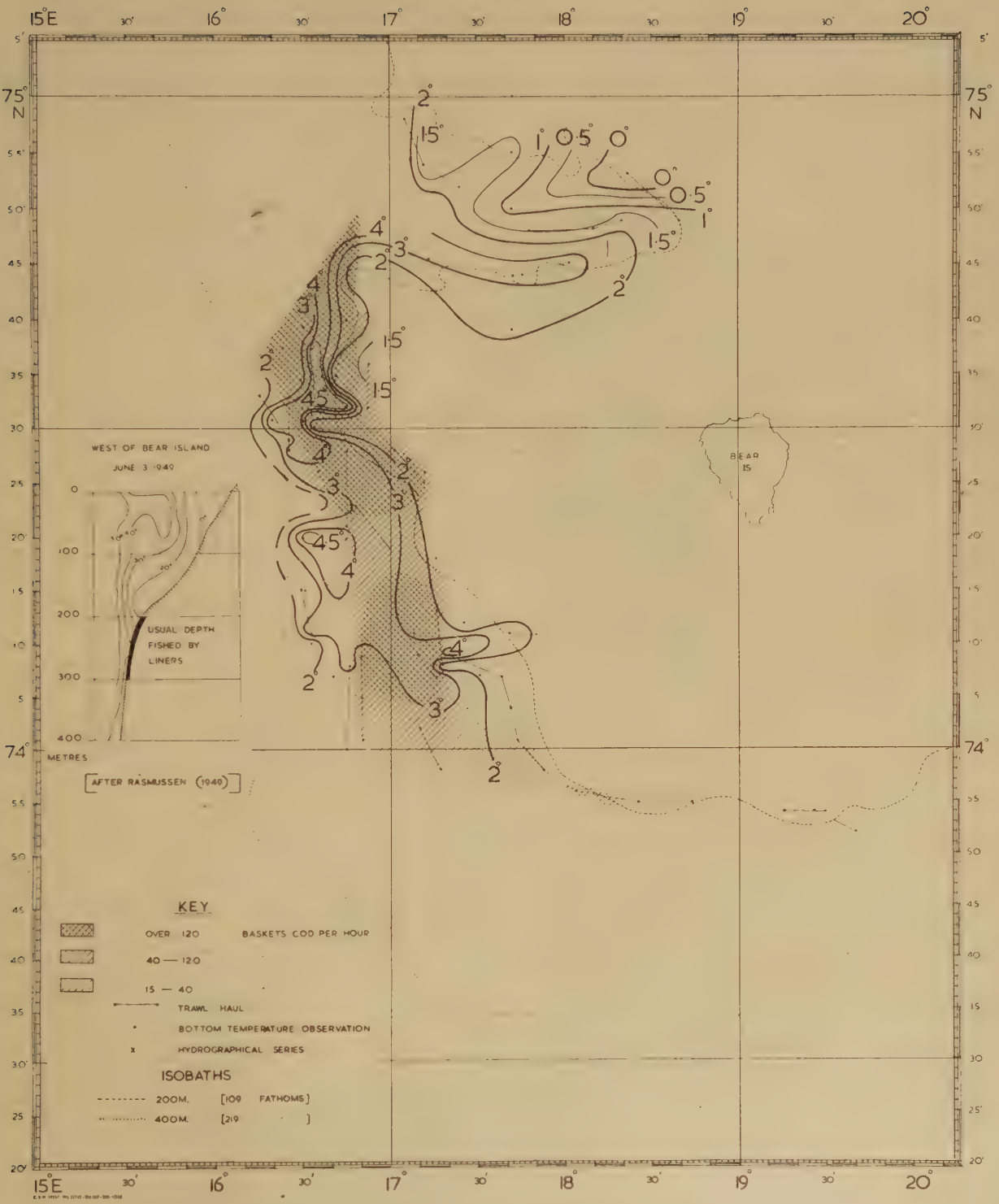


Fig. 12. Distributions of fish and bottom temperature in the Bear Island area, 31. May—6. June 1949.

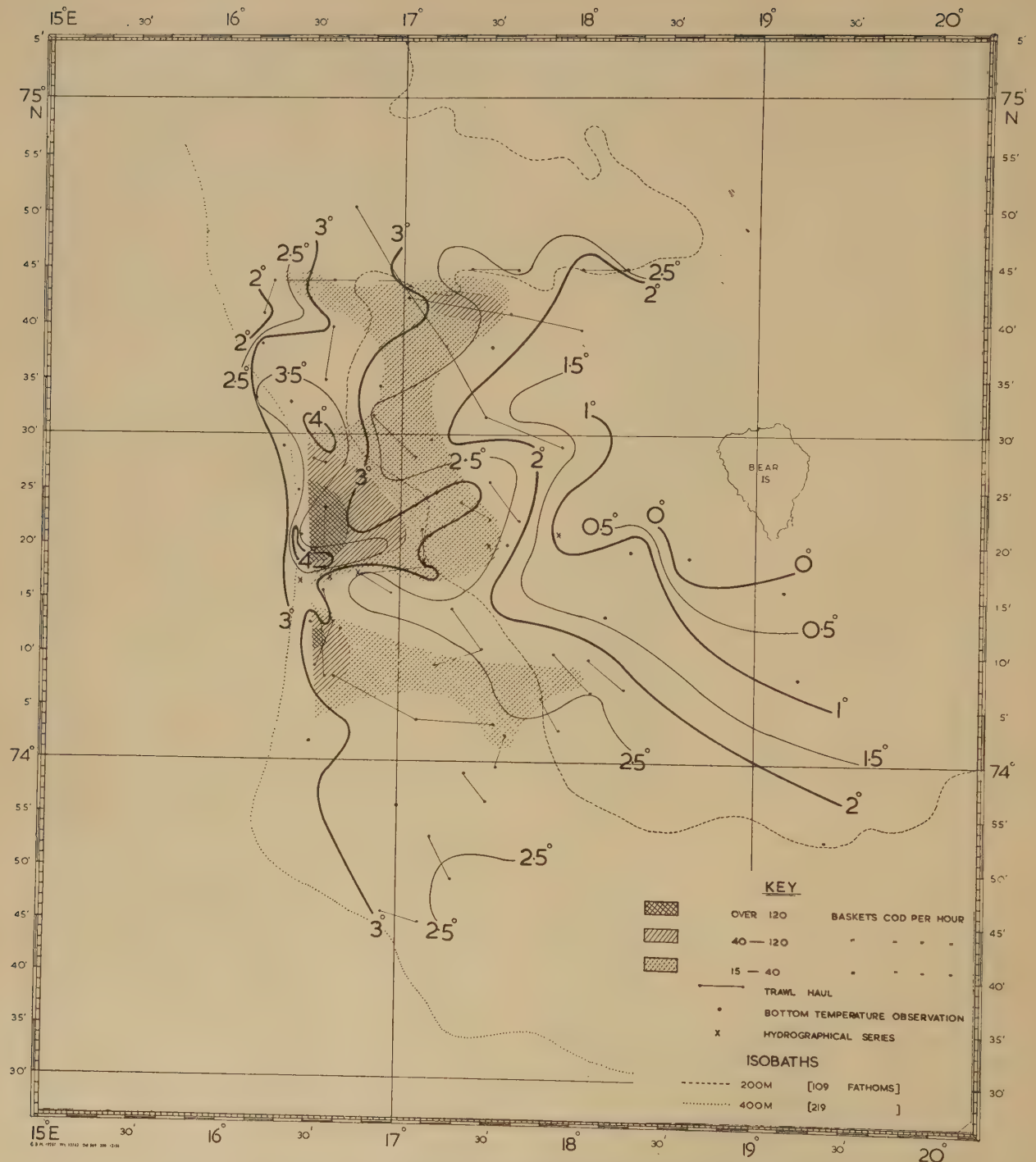


Fig. 13. Distributions of fish and bottom temperature in the Bear Island area, 27. May—5. June 1950.

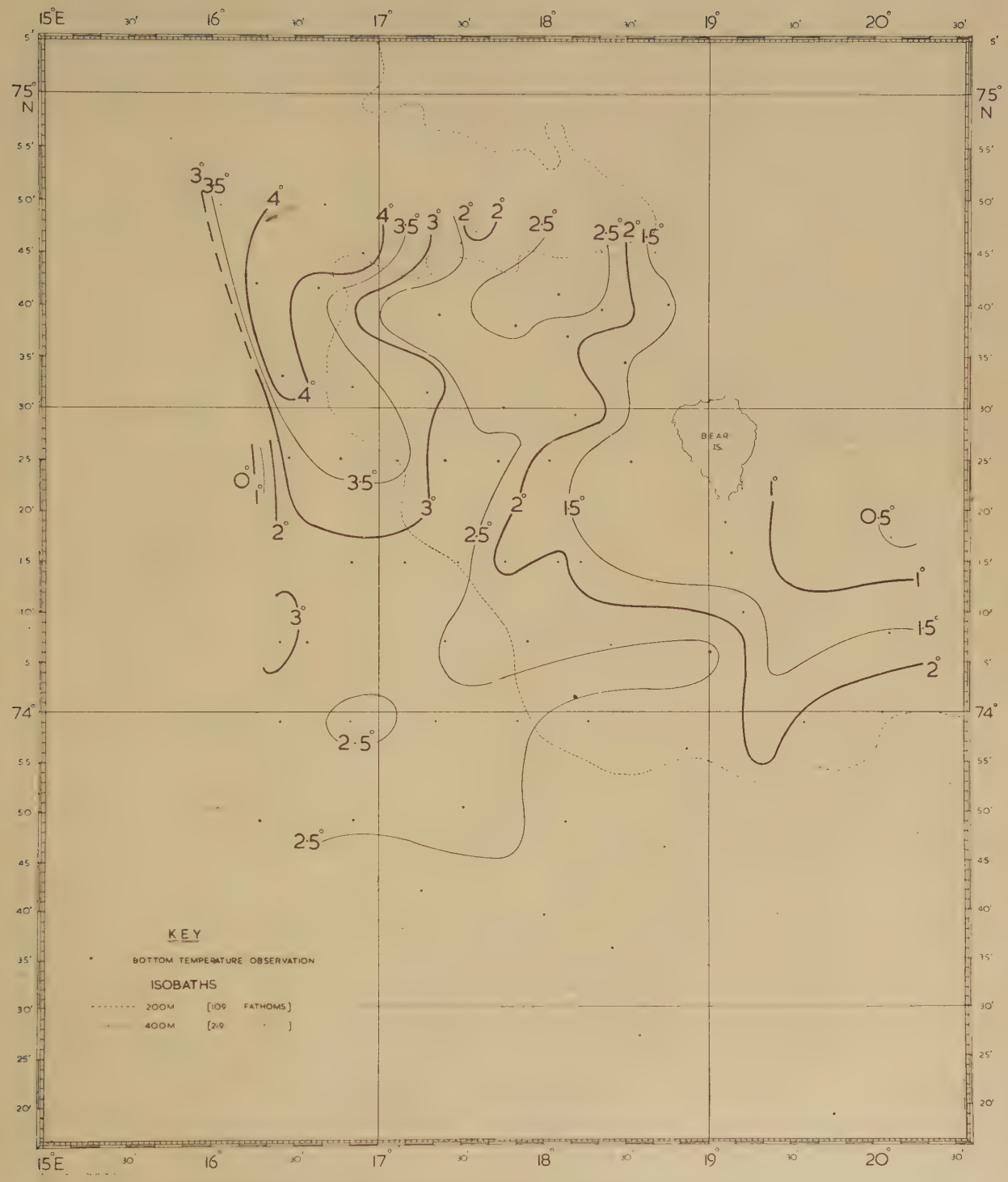


Fig. 14. Distribution of bottom temperature in the Bear Island area, 29. June—7. July 1950.

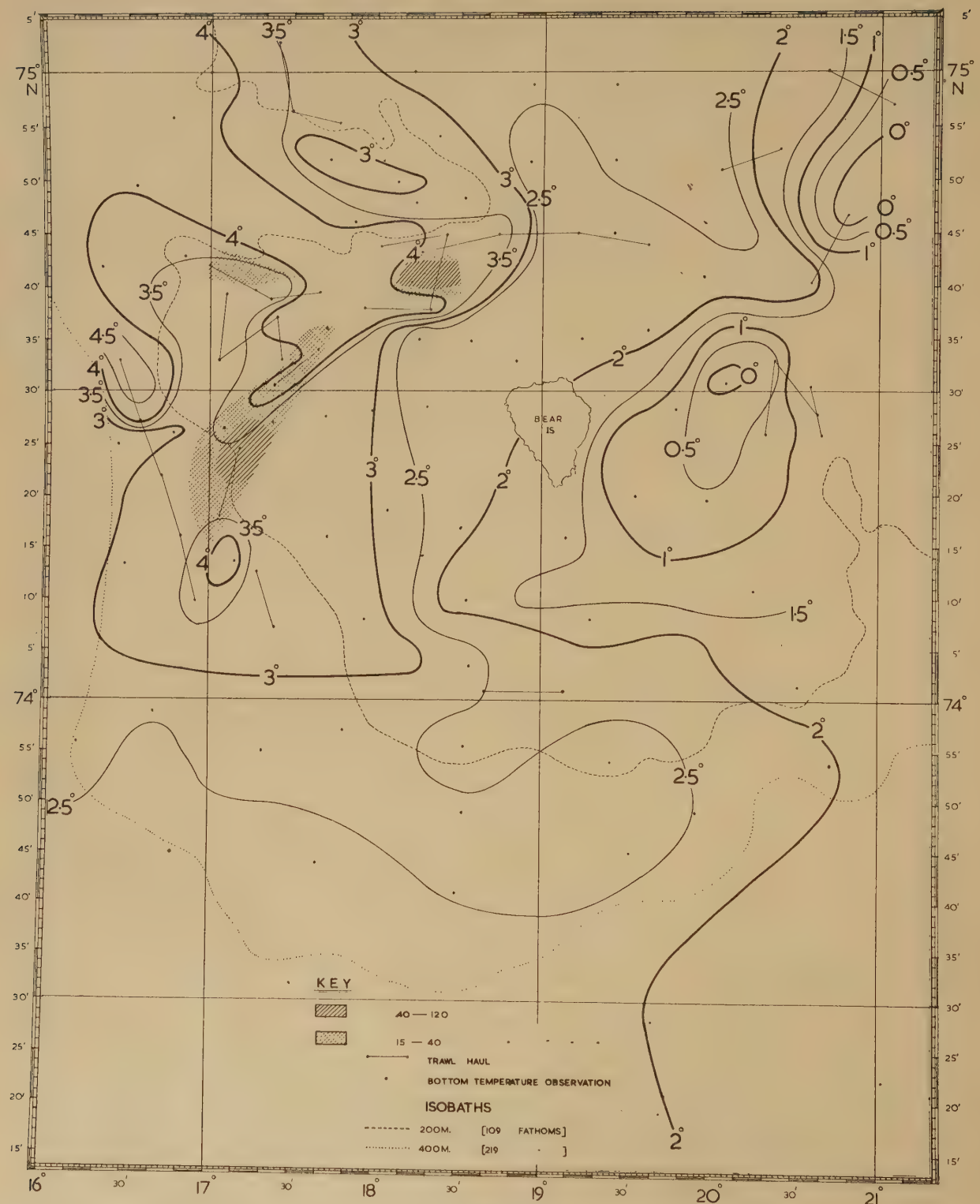


Fig. 15. Distributions of fish and bottom temperature in the Bear Island area, 4.—13. August 1950.

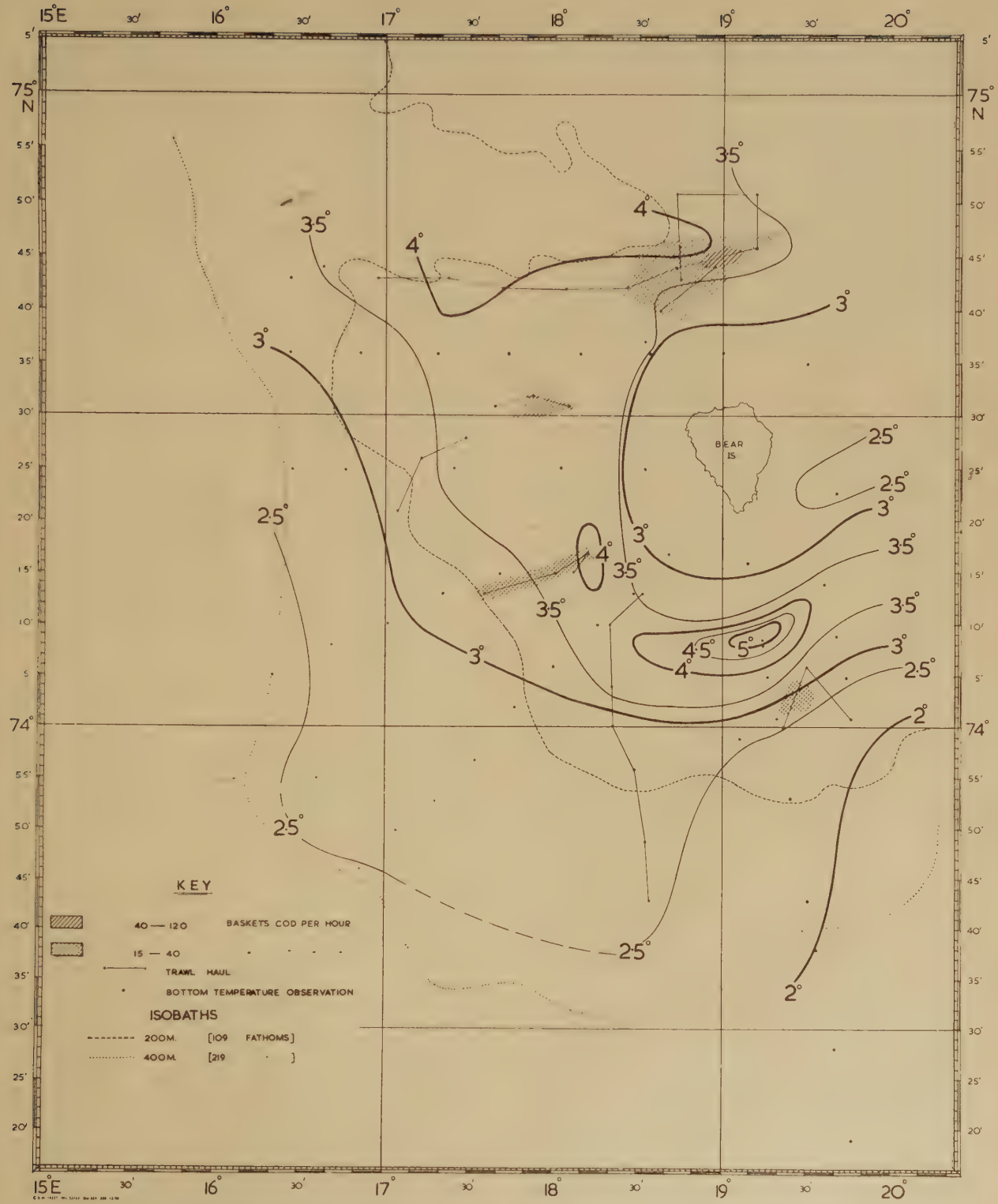


Fig. 16. Distributions of fish and bottom temperature in the Bear Island area, 2.—11. October 1950.

helicina, whose distribution seems to have been widespread at this time, and the cod do not therefore seem to have been influenced by the distribution of food.

In July 1949, however, the commercial fishery was taking place to the south-east of the island in 60—75 fathoms and the fish were found to be feeding heavily on krill. The paying fishing was then occurring in bottom temperatures between 1.5° and 2° C., the warmest part of a region of low bottom temperatures. Warmer water was found to the west of the island, but the hauls made by the R. V. "Ernest Holt" in this region yielded few fish and commercial ships also reported poor fishing hereabouts. As the fish taken to the west of the island were only feeding lightly, the abundance of cod at this time seems to have been affected by the feeding habits of the fish, but no plankton survey was made in order to ascertain whether the distributions of cod and krill were related.

August.

No cruise was made in the area in August 1949 but a wide bottom temperature and fish survey was made all round Bear Island during the period 4.—13. August 1950 and the results are given in Figure 15. The tongue of Arctic water had by then been displaced to the east and north-east and nearly all the western part of the bank was covered with water above 2° C.

The hauls made by the R. V. "Ernest Holt" showed that paying quantities of fish were again to be found along the southern edge of the North-West Gully and also to the west of the island in depths between 60 and 100 fathoms, the bottom temperature being between 3.5° and 4° C. The commercial vessels were fishing in the paying areas shown in Figure 15 and their reports indicate that their catches were at about the 40 baskets per hour level. They were also getting reasonable catches to the south of the island in depths between 60 and 70 fathoms, the bottom temperatures here being between 2° and 3° C. The fish over the whole of the area shown in Figure 15 were feeding lightly, except to the east and north-east of the island, where heavy feeding was occurring in cooler water.

October.

The Bear Island area was not visited again in 1950 until the period 2.—11. October. Another wide bottom temperature survey showed that water above 3° C. covered the whole of the bank to the south and west of Bear Island (Fig. 16). Lines of trawl hauls were made in various localities around the island, but paying quantities were only taken at the south-eastern corner of the North-West Gully in 65 to 85 fathoms, the bottom temperatures ranging between 3.5° and 4° C. The commercial trawlers were operating over a wide area and were reporting catches of about 40 baskets per hour, but spotty fishing, from the northern side of the North-West Gully, the South-East Gully and the area south of Cape Bull in depths between 70 and 95 fathoms, so that the distributions of fish and temperature were rather similar to those found in August.

The fish were once more found to be light-medium feeders and the main food was *Limacina helicina* and young herring (10—12 cm. long). Echo-sounder records showed that these latter made diurnal migrations, ascending to the surface at night and descending to the bottom during daylight. These records have been described by Burd and Lee (1951). If the cod were pursuing the herring, this may partly have accounted for the spotty fishing, but, as on the other cruises carried out in the area from May to August inclusive, there was no close association between the type or the amount of food and the size of catch, except in the area of high catches at the eastern end of the North-West Gully where herring was the main food.

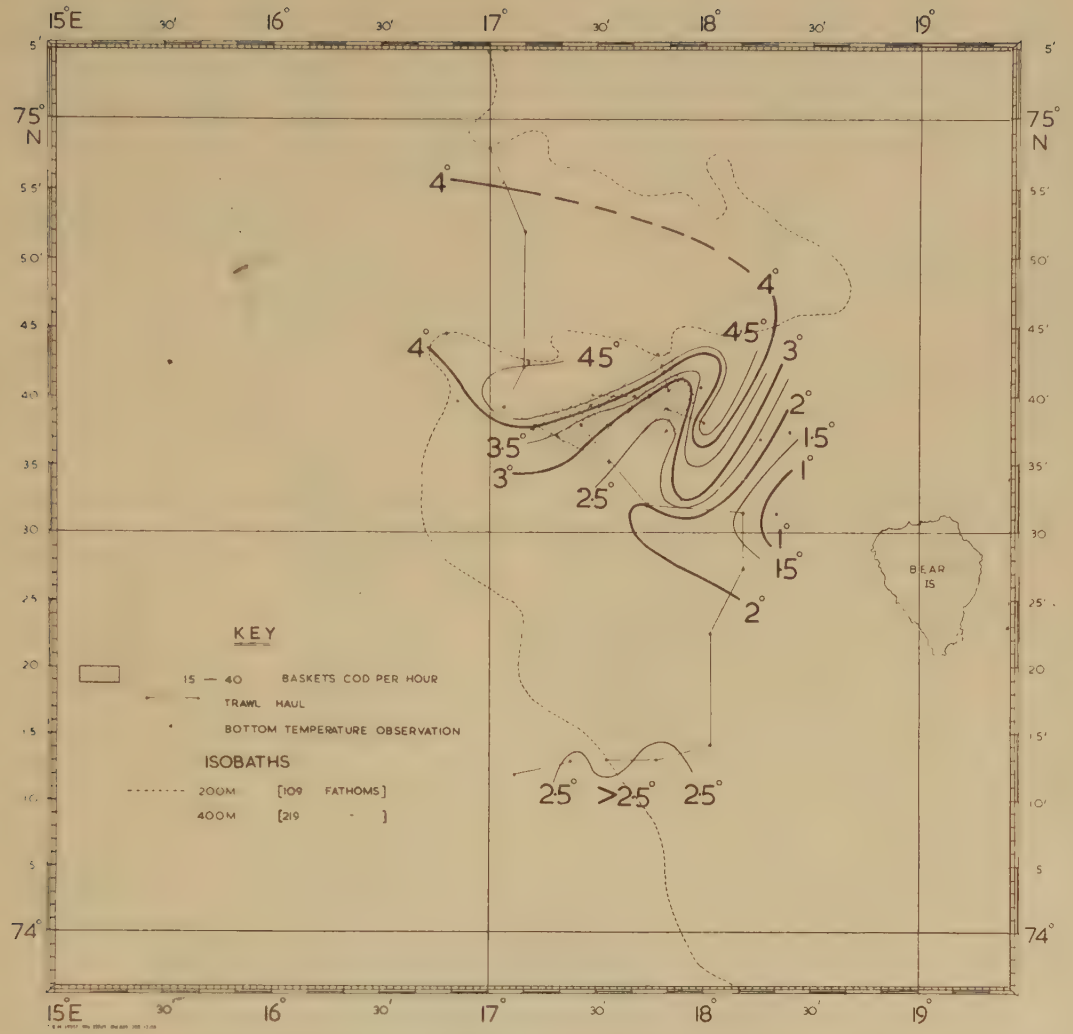
The results obtained during the summer and early autumn of 1950 thus show that the fishing reached a maximum at the end of May and in early June and then declined. At the same time the area covered by warm bottom water increased owing to the growing Atlantic influx. The decline of the fishing can be attributed to three possible causes. Firstly, the main body of cod may have moved away from the Bear Island area and, secondly, the increase in the area covered by warm water may have allowed the fish to disperse widely. Finally, the fish may have dispersed in order to feed, in accordance with Brotsky's views given above. Further work is necessary in order to determine which is the correct explanation.

The R. V. "Ernest Holt" also paid a brief visit to the Bear Island area during the period 15.—21. October 1949. Catches of cod in the small area sampled did not reach paying level, but a region yielding nearly 40 baskets per hour was again found on the southern edge of the North-West Gully. Here fish were taken in water of 60—70 fathoms with bottom temperatures between 2.5° and 4.5° C. Figure 17 shows that an anticyclonic eddy was located in this area and that steep temperature gradients existed. In such an area it is obviously extremely difficult to determine the effect of temperature on the distribution of fish, although in this case the higher catches do seem to have been associated with the upper end of the temperature range.

November-December.

Figure 17 shows that Arctic water was advancing across the Bear Island Bank in October 1949, but by November a new Atlantic influx had again brought warmer water to much of the bottom (Fig. 18). A cruise in the area during the period 20.—28. November 1949 produced an interesting distribution of cod.

From Figure 18 it can be seen that three paying concentrations were found, the major one being to the south of the island on Maslov's wintering grounds, in an area with bottom temperatures between 3° and 1.75° C. and in depths between 65 and 135 fathoms. Two minor concentrations lay to the west of the island in 80—90 and 120 fathoms respectively. The bottom temperatures in the former area were between 1.5° and 3° C., whilst the latter area was in Atlantic water with bottom temperatures between 3.5° and 4.5° C.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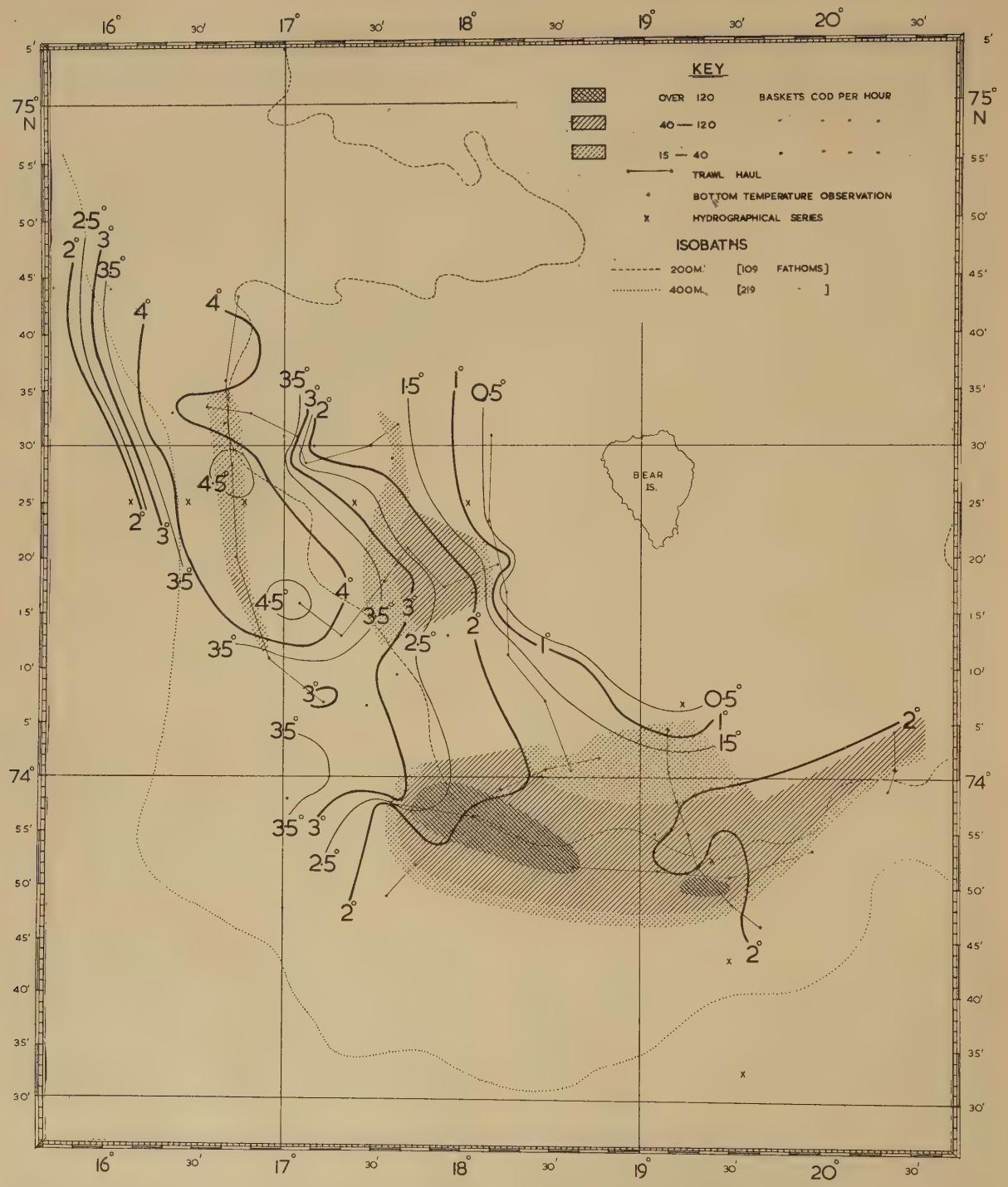

Fig. 18. Distributions of fish and bottom temperature in the Bear Island area, 20.—28. November 1949.

fixed, but it can be regarded as being approximately correct. The 1.75° C. surface isotherm has been plotted from thermograms. In the areas where it was situated to the south and west of the shallower 1.75° C. bottom isotherm, a temperature inversion existed with water below 1.75° C. overlying warmer water. One of these areas coincided nearly exactly with the major fish concentration and a vertical section through this area

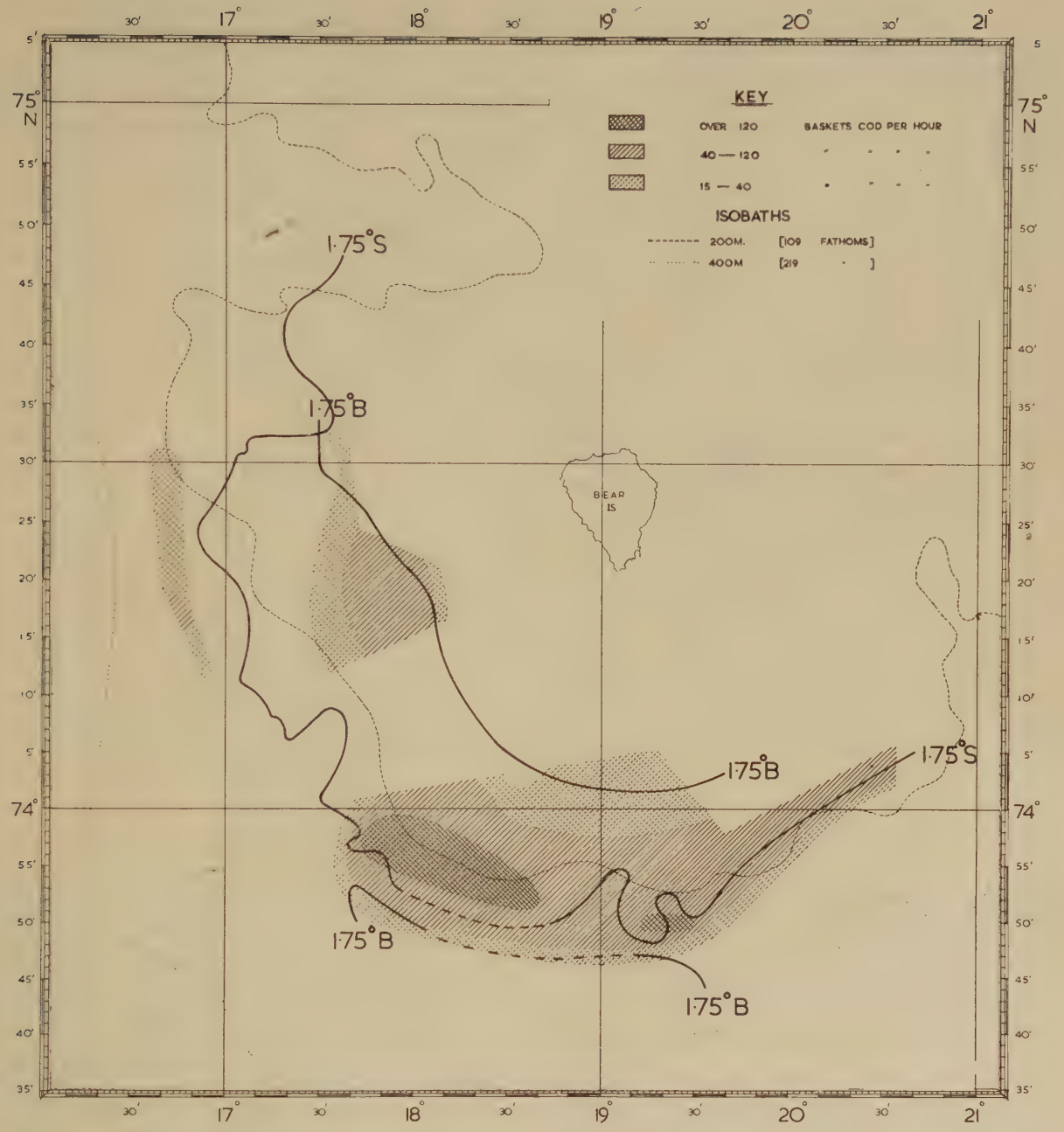

Fig. 19. Distribution of fish in relation to the temperature inversion in the Bear Island area, 20.—28. November 1949.

(Fig. 23) shows that the overlying cold surface water in conjunction with the bottom water below 1.75° C. could assist in concentrating the fish in a definite part of the sea-bed.

The overlying cold surface layer was also present to the west of Bear Island but it only covered a minor fish concentration. However, the deeper 1.75° C. bottom isotherm was not situated close to a shallower one in this area (Fig. 5) and one of the confining factors was therefore absent. It must also be noted that the total range of the bottom temperatures on the southern part of the bank was small and that the hypothesis therefore implies that the cod are sensitive to differences of temperature of less than 0.5° C. Moreover, the pattern of the hauls carried out did not critically test the relative effects of the positions of the 1.75° C.

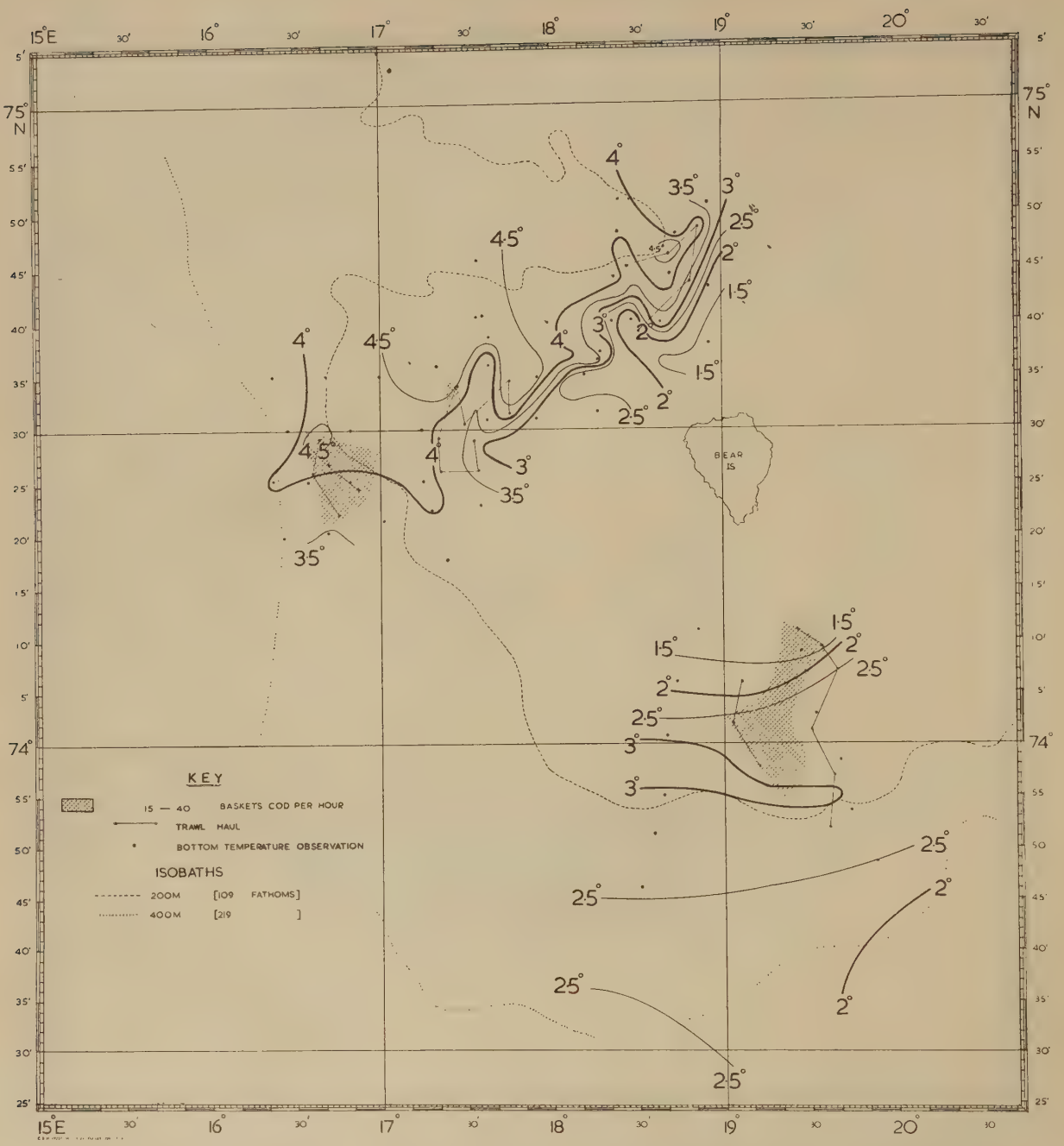

Fig. 20. Distributions of fish and bottom temperature in the Bear Island area, 14.—22. November 1950.

bottom isotherms and the 1.75° C. surface isotherm. Nevertheless, the hypothesis appears to be promising and worth further investigation.

It was hoped to do this in November 1950 but, as described above, the temperature inversion was later in developing in this year. Figures 20 and 21 show the increasing Atlantic influence in this month and also that paying quantities of fish were not encountered. It is tempting to assume that the absence of cod was due to the absence of two of the concentrating factors south of Bear Island, viz., the temperature inversion and the deep water with a temperature below 1.75° C., but there is also some evidence that the fish were late in arriving in the Bear Island area during the winter

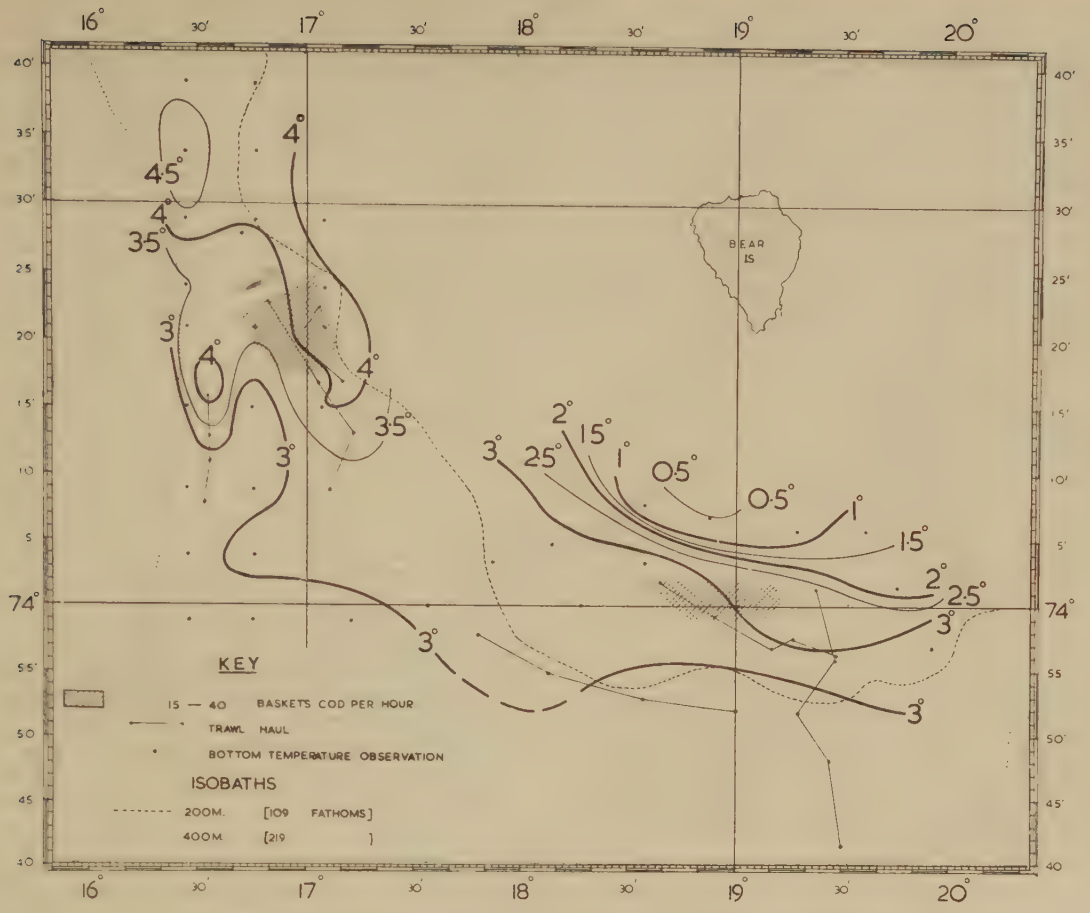

Fig. 21. Distributions of fish and bottom temperature in the Bear Island area, 27. November—4. December 1950.

of 1950—51. Commercial fishing was carried on to the north of Hope Island in the autumn of 1950 until much later than usual and it may be assumed that the fish were late in leaving the Hope Island and Spitsbergen grounds on account of the high bottom temperatures prevailing at that time. Reports from commercial ships also show that heavy catches were being taken in deep water to the south and south-west of Bear Island between January and March 1951, so it would appear that the fish did not arrive at Bear Island until at least mid-December.

January-March.

The temperature inversion present in November 1949 was found to persist into January 1950 but to be irregular and to cover a smaller area. The paying concentrations found during the period 11.—20. January were taken where an inversion existed, but the whole area covered by the inversion did not yield fish. Figure 22 shows that bottom temperatures had increased since November and that two paying concentrations were located in 65 to 140 fathoms to the south-east of Bear Island in the band of maximum warmth with temperatures between 1.5° and 3° C. The two groups were separated by a tongue of cold water, a situation similar to that found west of Bear Island in May 1950, but the fishing was so variable and the hydrographical structure so complex at this time that it would be unwise to make any inference on this occasion.

Commercial vessels took good catches in 60—150 fathoms at many points to the west and south of the island, the bottom temperatures in these regions exceeding 2° C. (Fig. 22). In all cases, however, the fishing was variable and it might be inferred that the increased Atlantic influx had encouraged dispersal, since it had weakened those factors, which according to GRAHAM's hypothesis concentrated the cod in the previous November. There was a larger area of warm bottom water and the temperature inversion was breaking down. Moreover, the cruises carried out in February and March 1950 showed a further decrease in the area covered by the temperature inversion and

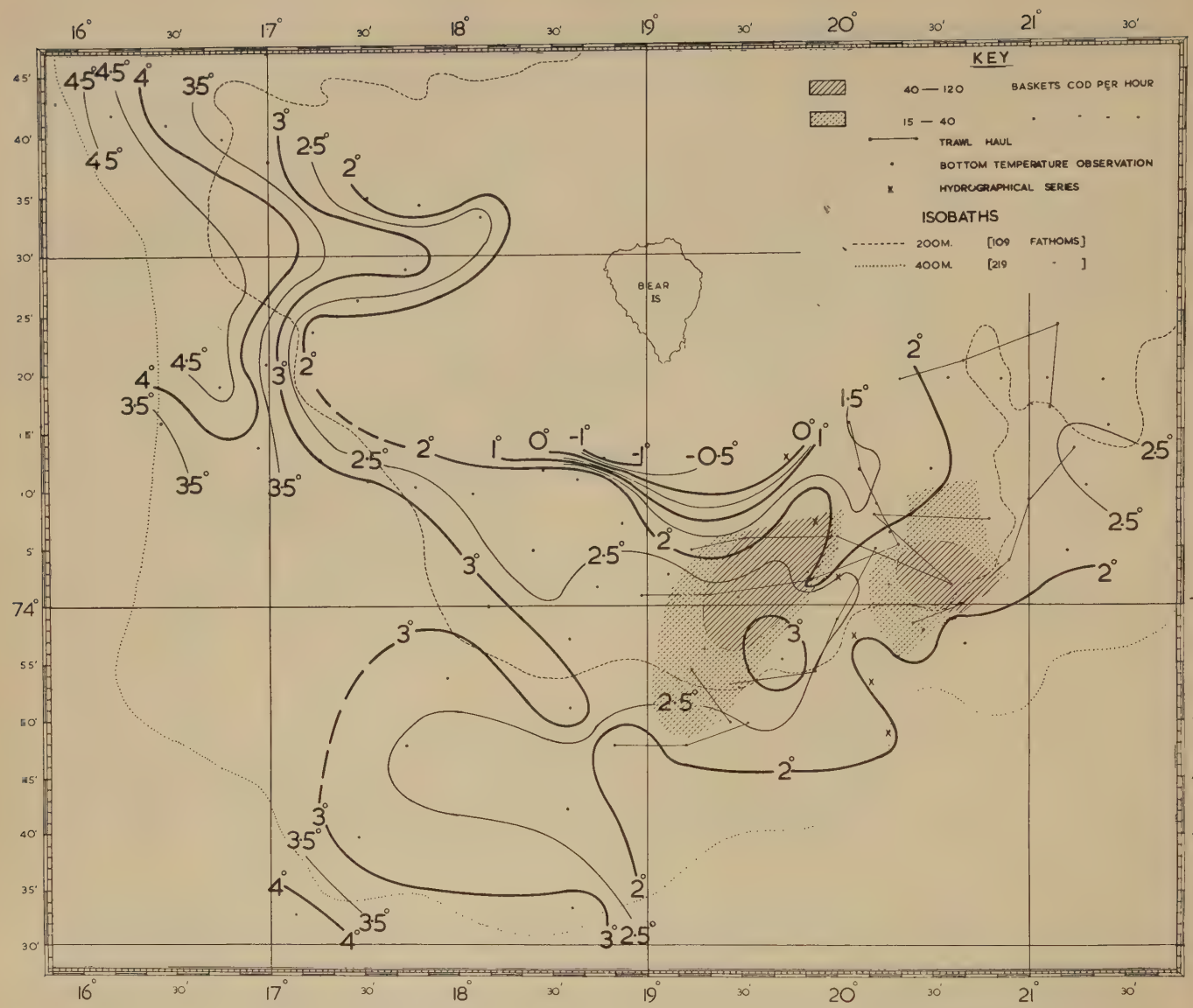

Fig. 22. Distributions of fish and bottom temperature in the Bear Island area, 11.—20. January 1950.

also failed to reveal any substantial paying concentrations of cod. The Atlantic influx weakened in these months and the temperature and area of the warm band on the shelf south of Bear Island both decreased, but the decrease does not seem to have been sufficient to have assisted in concentrating the fish. It is possible that the cod may have moved out of the area, as in April 1950 they were found in paying quantities in water above 2° C. at least 90 miles east of Bear Island, as described above.

Information for Fishermen.

It has been possible at this stage of the work to give some information to fishermen about the use of thermometers; for example, that paying quantities of fish are rarely taken in temperatures less than 1.75° C., except in summer when the fish are feeding heavily in the area to the east of Bear Island. Furthermore, in May—June there is very heavy fishing west of the island when there appears to be some association between the fish and Atlantic water. The heaviest catches at this time seem to be taken in temperatures between 3° and 5° C. A fisherman using this information would quickly have found paying quantities of fish in May—

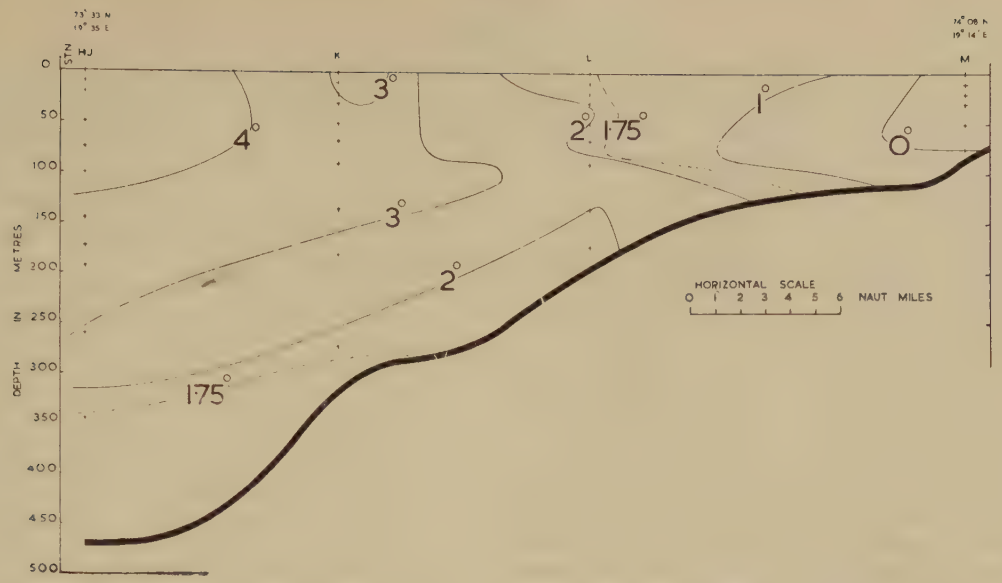

Fig. 23. Distribution of temperature along the South Bear Island Section, 26. November 1949.

June 1949, when the fishing was concentrated in a narrow, well-defined band of warm water. In 1950, however, the band was wider and the boundaries were less well-marked and a fisherman using a thermometer in this year would not have located paying concentrations as quickly as in 1949.

Very heavy fishing occurs again when the fish are south of Bear Island in the winter months. The time when this takes place seems to vary from year to year, but the fish in this area appear to be located in a band with a temperature between 1.75° and 3° C. The temperature of the upper layers may have some effect at this time, but the bottom temperatures should be a sufficient guide to trawlermen.

At other times of the year the fishing is not so heavy and more spotty. From August to November the heaviest fishing west of the island seems to be in temperatures between 3.5° and 4° C. However, as the area covered by water between these temperatures can be extensive and the fishing is spotty, a fisherman using these temperatures as a guide in these months may be a long while in finding paying fish. The situation in the period February—April is not clear, but the fish seem to be located between points south-west and south-east of the island in temperatures above 1.75° C., and they appear to be concentrated in deep water towards the west if the temperatures on the southern flanks of the Bear Island Bank and in the eastern part of the Bear Island Channel are below this critical temperature.

It is apparent that there are two suitable temperature ranges which operate in different times and places. The 1.75° to 3° C. range applies mostly to the region south of Bear Island, whilst the 3° to 5° C. range applies to the area west of the island. As the cod which, according to Trout's hypothesis, migrate between Bear Island and Hope Island move in an area with low bottom temperatures compared with the cod which migrate between Bear Island and Spitsbergen, it might be thought that the two types of cod are associated with the two temperature ranges. Trout's otolith studies have as yet failed to show that this is the case, except for the samples collected in November 1949.

Conclusion.

The hydrography of the Bear Island region appears, therefore, to have some influence on the fishery but it has been shown that it must be considered in conjunction with other factors. At certain times the hydrographical structure seems to assist in concentrating the fish in certain localities and it is possible that at other times it may encourage dispersal, but this latter possibility will need further examination when marking experiments have given more information about the migrations of the cod. There is also a possibility that the timing of these migrations may depend on the strength of the Atlantic influx into the area. It is obvious that the work is far from complete, but the progress made so far appears to be promising and the policy of attacking the problem by using a team consisting of hydrographers and biologists, who all work in close collaboration both in the field and ashore, would appear to be justified.

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13.

A Contribution to the Study of the Migrations of the Atlanto-Scandian Herring.

By

Finn Devold.

Since G. O. Sars in 1873 (4) formulated the hypothesis that the open ocean was the home of the great Norwegian tribe of herring, it has been one of the major problems in Norwegian herring investigations to verify this hypothesis. On the first cruise of the research ship "Michael Sars", in 1900, Johan Hjort worked on the problem. He, also, found herring in the open ocean, and in his report (3) of the cruise he concluded that there were continuous herring shoals from the west coast of Norway to Iceland in the summer of 1900. A fish merchant from Ålesund pursued these herring, with some success; but as the expenses exceeded the income from the expedition, the experiment was not repeated.

Johan Hjort pays great attention to the area north of the Faroe Isles, and to the border region of the

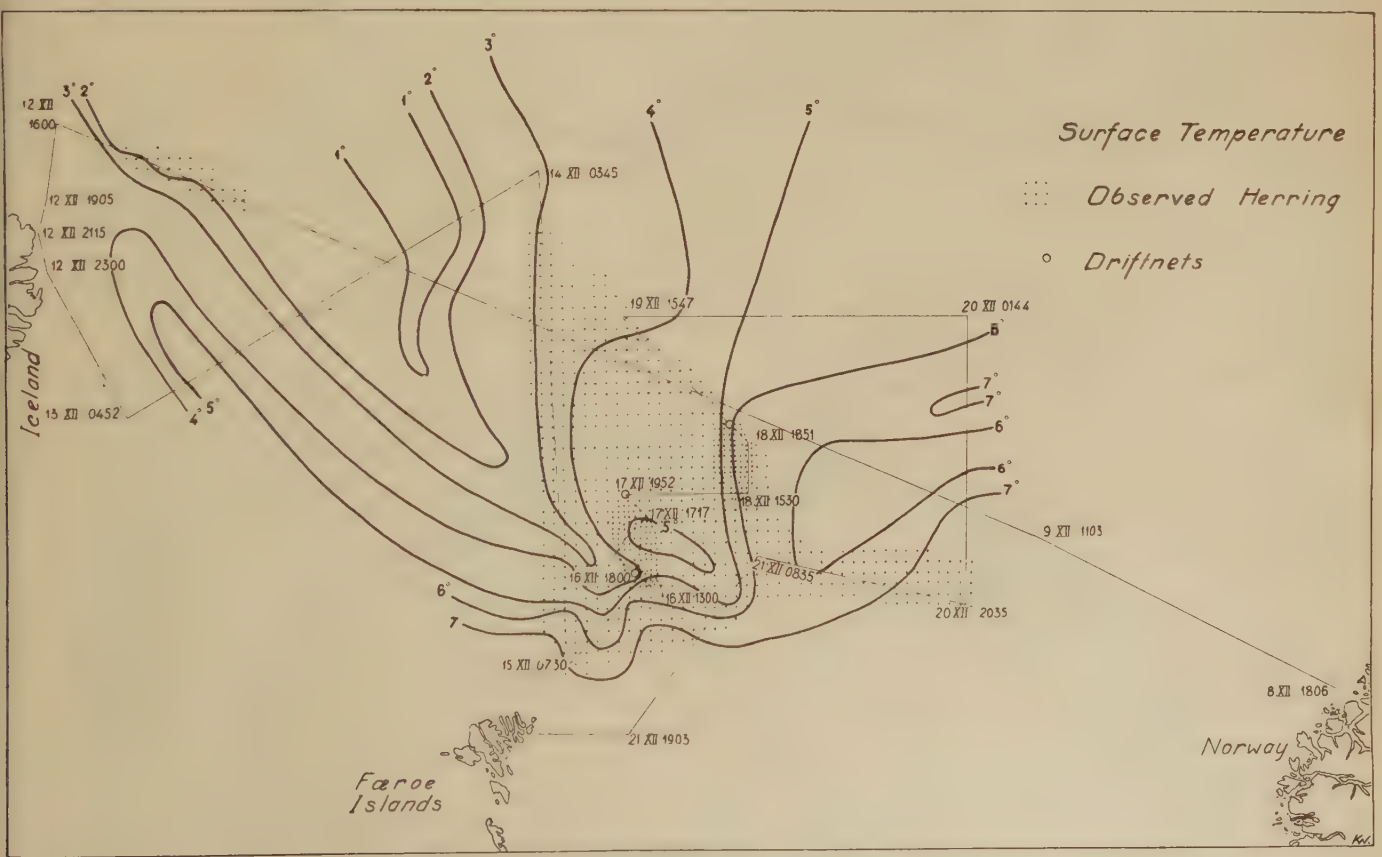

Figure 1. G. O. Sars Cruise 8.-21. XII. 1950.

East Icelandic Arctic Current, since these areas, as he shows, afford living conditions not only for plankton, but also for higher animal life. Unfortunately, JOHAN HJORT did not pursue the work which had given such promising results the first summer. The banks were of greater interest and importance, and at that time many banks, which today are important fishing grounds, were not tried or known at all.

When the Norwegian fisheries scientists lost their sea-going research ship at the start of the first world war, it was impossible to continue the investigations in the open sea.

In 1948, Dr. VEDEL TÅNING on board the Danish research vessel "Dana" managed to catch about 1000 pounds of herrings north-east of the Faroe Isles. A sample from this catch was examined at our laboratory, and it was established that the sample consisted of mature herring of the Norwegian tribe.

In 1949, we were able to hire a sea-going ship for special herring investigations, and during the cruise herring were caught north of the Faroe Isles, off the north coast of Iceland and in the Jan Mayen area. All samples show the same picture as to age distribution, size, number of vertebrae etc., and the results of the investigation support the theory, advanced by Mr. ÁRNI FRIÐRIKSSON (1), that the main part of the herring caught off North Iceland belongs to the Norwegian tribe of herring. The herring in the Jan Mayen area are of the same tribe (DEVOLD, 1950).

In 1950, we were far better equipped for the search for the herring shoals in the open sea, having acquired the new research vessel "G. O. Sars". This ship is equipped with a special ASDIC instrument, which makes it possible to locate a herring shoal of medium size at a distance of more than one nautical mile from the ship. At the meeting in Copenhagen last year, this author gave a brief review of the results of the cruise in the summer of 1950. Here will merely be repeated that herring were found mainly on the east side of the East Icelandic Arctic Current; and further, that it was reasonable to conclude that the herring, after spawning off the Norwegian coast, spend a month or two in the area north and east of the Faroe Isles, moving northwards later in the summer on both sides of the Arctic water coming southwards between Jan Mayen and Iceland. Herring shoals were not discovered in the cold water. If the hypothesis that the herring move northwards on both sides of the East

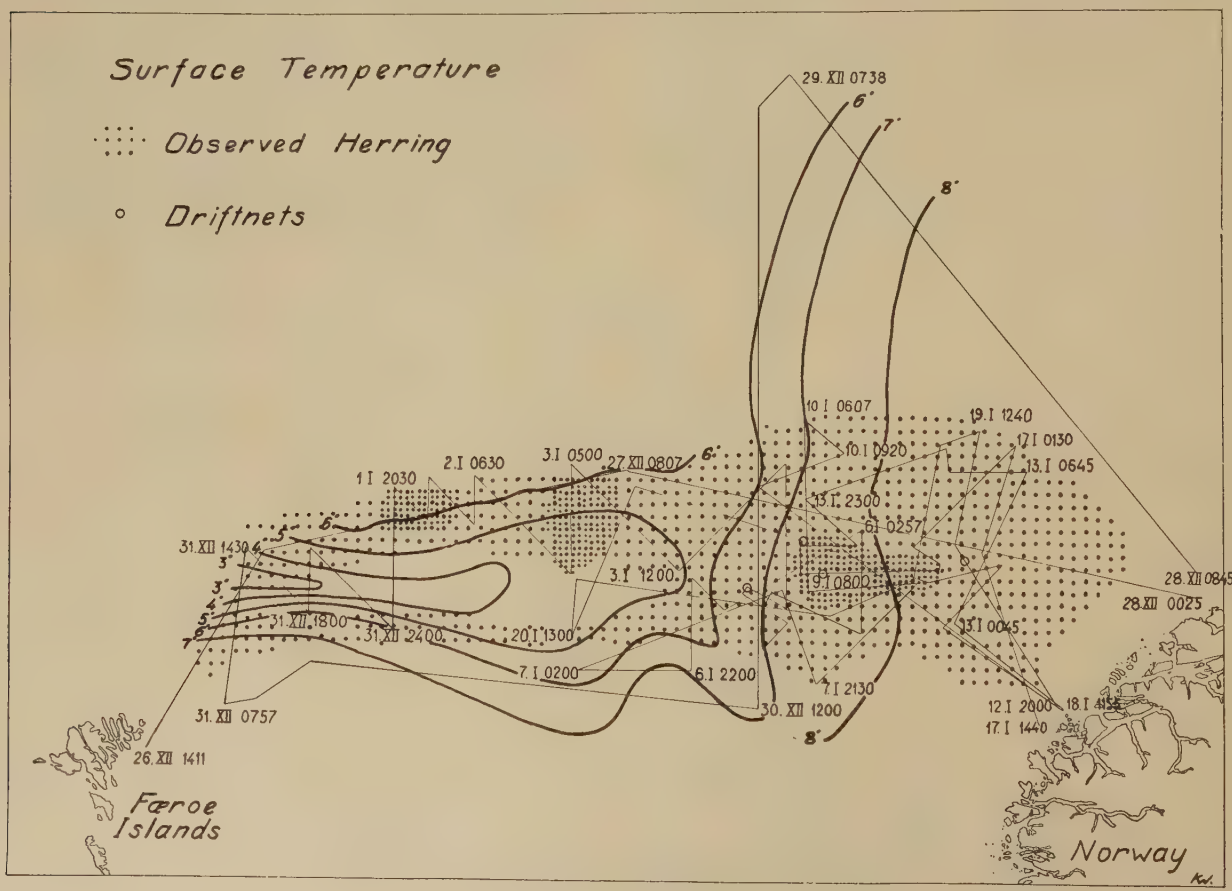

Figure 2. G. O. Sars Cruise 26. XII. 1950—22. I. 1951.

Icelandic Arctic Current is correct, it should be possible to make a survey before the herring fishing north of Iceland starts, and thereby determine whether the main part of the herring will be located on the east side of the cold water. In such a case, the natural route of the herring will take them into the area round Jan Mayen. Alternatively, if great herring masses are discovered on the west side of the cold water, they will continue northwards and enter into the Icelandic coastal waters. When this occurs, it is reasonable to believe that the fishing north of Iceland will be good. If the conditions mentioned first prevail, the result will be a poor season.

We do not know, how far north the herring penetrated in the summer of 1950 and, at that time, we did not know anything about the route of the herring back to the spawning places off the Norwegian coast.

The Russian biologist, F. I. Glebov (2), published a remarkable paper in 1938 on the small and fat herring off the Murmansk coast. He concludes that, when in the summer, the temperature from the ocean into the fjords is rising, great invasions of herring may take place. In the winter, the opposite is the case; the temperature must be higher out at sea than in the fjords for such invasions of herring to take place. The explanation he gives is that the herring during the summer, being in their feeding stage, will take their food in relatively warm water, where all metabolic processes are increased and therefore go into the fjords. In the winter, little or no food is available for

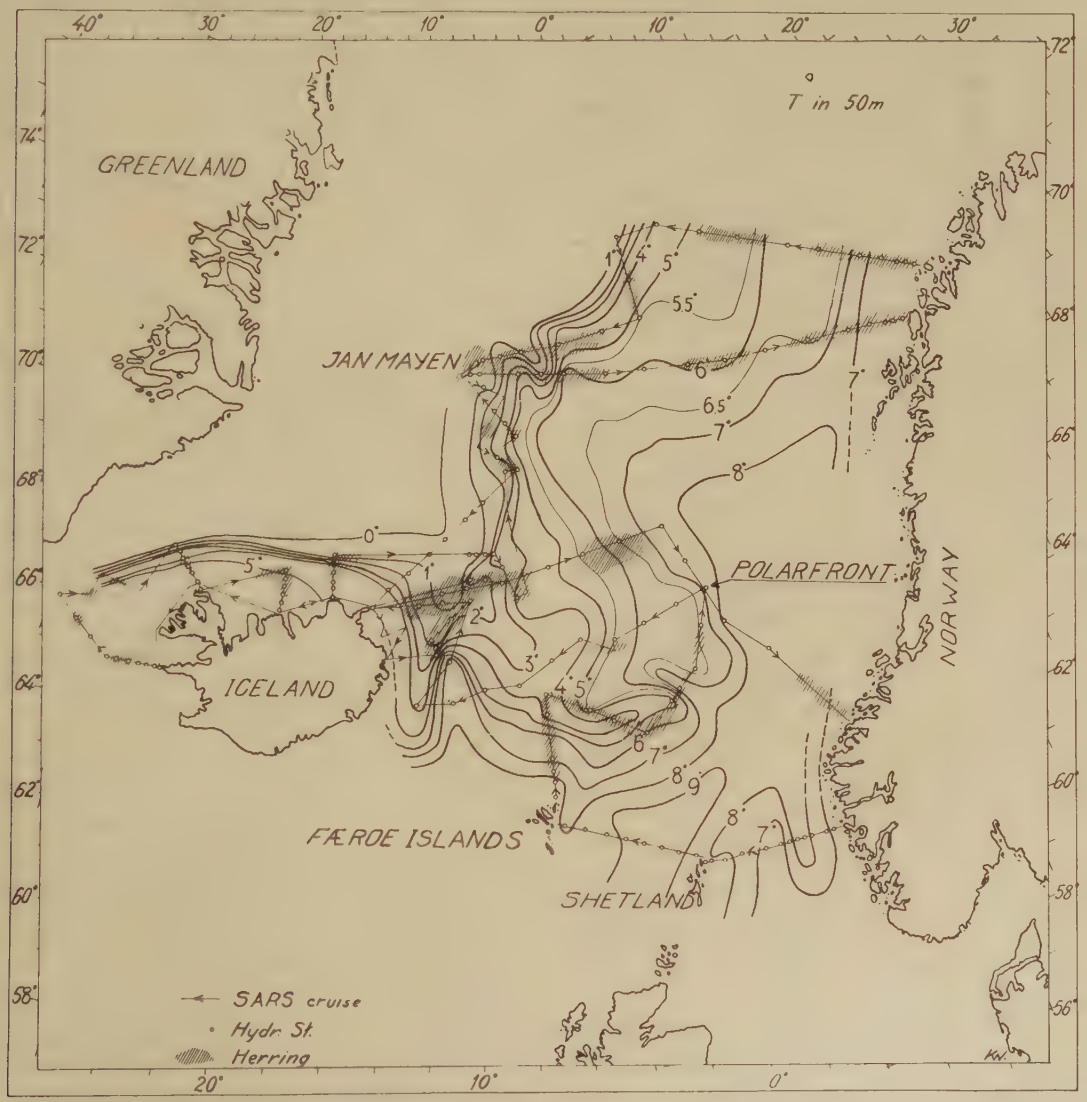

Figure 3. G. O. Sars Cruise 23. VI. — 1. IX. 1951.

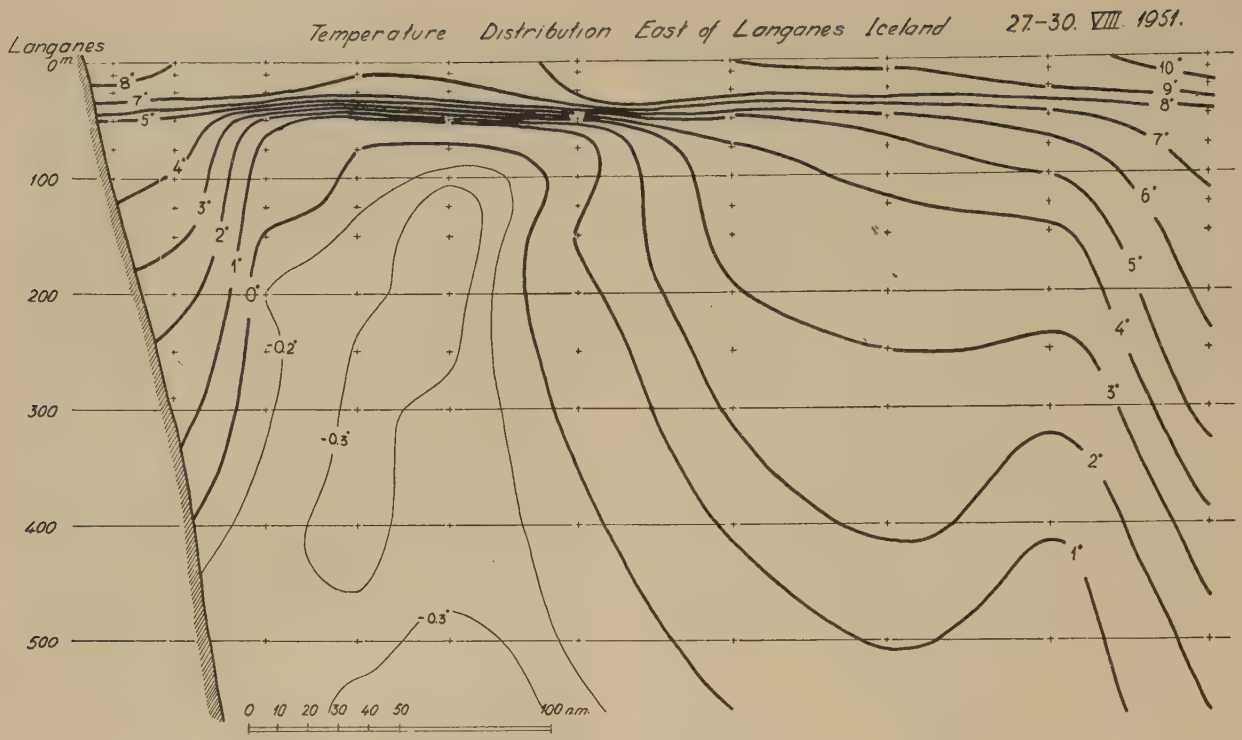

Figure 4. True Direction 80°.

the herring, therefore they seek cold water, where the fat reserves are more slowly broken down. If this theory is correct, it seemed likely that the large mature herring living on the edge of the cold Arctic water of the East Icelandic Arctic Current would go into the cold water and thus move towards the Norwegian coast.

In the winter 1950/51, we tried to investigate this question. We found the herring in the cold water north of the Faroe Isles before Christmas. At this time, no herring were located east of the zero meridian, and the main bulk was located farther to the west. After Christmas, the herring seemed to follow the narrow channel of cold water penetrating eastwards towards the Norwegian coast, as will appear from Figures 1 and 2. On these maps the hatched areas indicate where herring were found, and the surface isotherms are given. In the winter, the upper layer is fairly homogeneous, and the isotherms give a good picture of the temperature conditions in the water layer in which the herring were migrating. When the herring shoals reached the Gulf Stream, about 100 miles off Møre, they came to a stop, and eventually went through the warmer Atlantic water into the Norwegian coastal waters.

Late in June 1951, we again found the herring north of the Faroe Isles. Figure 3 shows the route of the "G. O. Sars", the hatched areas giving the positions at which herring were found. The isotherms are those for a depth of 50 metres. As will be seen, there is warm water close to the Icelandic coast, then a cold tongue, and farther east there is a trough in the cold water masses filled with a tongue of warmer water. Then comes the main part of the cold water, followed by Atlantic water on its east side. Although herring shoals appear to be located in the cold water, they are actually living in warm water, as the cold water shown in Figure 3 is covered by warm water. East of Iceland herring were not found deeper than about 30 metres. The section in Figure 4 shows the temperature east of Langanes, Iceland.

Figure 5 shows typical recordings of summer herring shoals, and gives the temperature distribution at the place. The herring are located in the warm water above the cold water.

When we first approached the Icelandic coast in the summer of 1951, we found the banks east of Langanes covered by cold water. We therefore believed that the herring season north of Iceland would be a poor one. We also made investigations on the west side of Iceland, in the Denmark Strait, and here we located herring shoals in the border region between the warm Atlantic water and the icy water of the East Greenland Current. We were, however, not able to catch these herring, as they were found at a depth of about 70 metres. The hydrographical conditions give a reasonable explanation why the herring were found at such a great depth. The Polar water has a low salinity due to the melting ice, and, in spite of its low temperature, it is therefore lighter than the

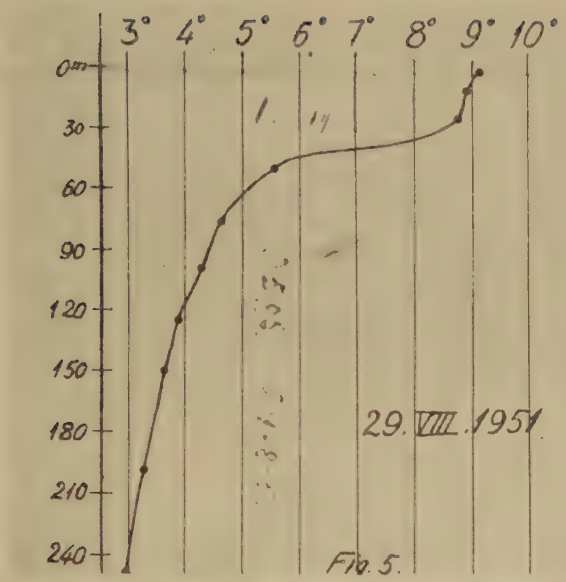

Figure 5. Typical Recordings of Herring Shoals.
The graph gives the temperatures at the different depths.

Atlantic water, and will consequently form the surface layer. As long as such conditions prevail, the herring will be located fairly deep, and the fishing possibilities will be poor with ordinary gear.

Off East Iceland the warm Atlantic water is lighter than the cold Arctic water forming the East Icelandic Arctic Current, and the herring in this area are consequently in the summer living in the surface layer. The chances of catching the herring are therefore good.

On our return to East Iceland, it was found that great alterations had taken place in the hydrographical conditions. A warm-surface layer was now covering the cold water over wide areas, and many small herring shoals were recorded as penetrating into this layer. The season off North Iceland therefore became fairly good; but the main part of the herring was found above the cold water far from the coast. We reported the conditions to the Norwegian drifters, and this year they did follow our advice. During August, the fishing took place in the open ocean up to 150 miles off the Icelandic coast.

Apparently the investigations carried out during the last few years by Denmark, Iceland and Norway have revealed the main routes of the herring in the open sea. But Figure 3 shows that we also found vast concentrations of herring off the coast of North Norway. The first 200 miles from the coast were occupied by the 0- and I-groups, but 250 miles out, we found large mature herring. It is not likely that these herring have covered the long route from the west coast of Norway to the Faroe Isles, Iceland and Jan Mayen to arrive here by the end of July. Every year in May, we receive reports of herring off the Lofoten islands. It is likely that there is also a northerly route for the herring leaving the coastal waters off Lofoten or Vesterålen. Whether it is the herring taking the latter route which first arrive in the Jan Mayen area, we do not know. We still have not found the younger year-classes, which constitute the main part of the mature herring stock. We do not know where the fat herring live, but on next year's cruise we will try to answer this very important question. It is probable that by starting the investigations off the North Norwegian coast in May, and working in the area north of the line Lofoten—Jan Mayen, and perhaps also investigating the Barents Sea, we may approach the solution of this problem.

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14.

The Scottish Programme of Herring Hydrography, 1951.

By

R. E. Craig

The Marine Laboratory. Aberdeen.

During the period of the 1951 summer herring fishery off the east coast of Scotland, an intensive programme was carried out by the research vessel "Clupea". So far as weather conditions have permitted, a survey was made during every second week from 22. April to 29. August. The echo-sounder was used continuously in a search for herring concentrations and on every survey, at 74 stations, temperature and salinity samples were taken at surface, 10 m., 30 m. and near the bottom. Plankton sampling was carried out at each station with both the Hensen net and the plankton indicator, the indicator sampling being made on behalf of the Scottish Marine Biological Association Laboratory in Leith, whose staff are comparing these data with the catches from commercial vessels. It is hoped that such surveys, if continued more intensively and extensively, may give better understanding of the factors determining herring movements within the fishing area, and those determining the success of brood survival.

While it will be clear that no more than preliminary study of the results has yet been made, it may be worth while to make some preliminary observations, in the knowledge that they must be re-examined much more thoroughly, in conjunction with other data as they become available.

The current system of the area has already been studied (Tait, 1934) and in Figure 1 I have presented the main current streams modified in the light of the temperature and salinity data. Complex eddy systems are formed by the convergence of these streams and the temperature picture varies considerably from week to week. The salinity pattern shows less variation, but overall changes of salinity of the order of 0.2 $^{0}/_{00}$ have occurred. The surface distribution of temperature has not a very close correspondence to that of the underlying layers, particularly in the early part of the season. The influence of wind direction and force on this situation and in relation to this fishery will be studied.

The most immediate study possible was that of the relation between surface temperature and the distribution of herring. Some degree of positive correlation was obtained in this way, including coincidence between an incursion of relatively warm surface water from the east, and the major herring movement during the fishing season. This correlation having been observed, it was natural to extend the examination to the lower water layers at the 10 and 30 metres in which the herring most often feed. Such correlation as occasionally exists is but a shadow of the surface temperature fit, and is much less close.

On the charts (Figure 2) for Surveys 2—10 are plotted a) the surface isotherms, and b) the boundaries of the principal herring concentrations as determined

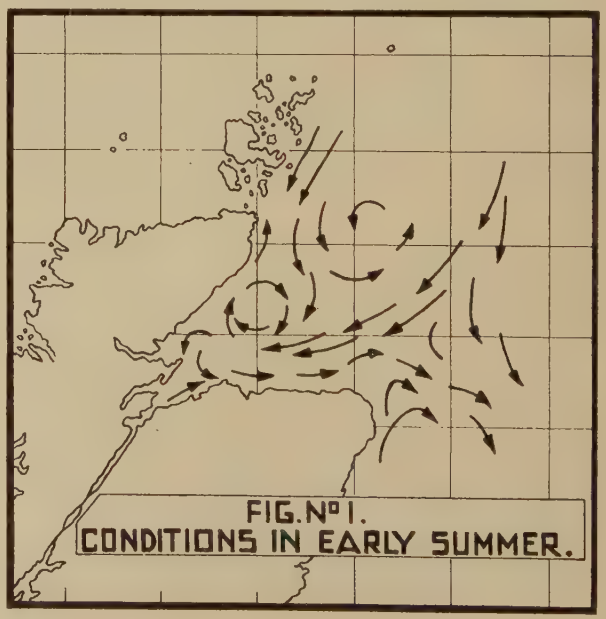

Figure 2. Scottish East Coast Herring Fishery 1951.

a) Pecked lines — Surface isotherms,

b) Hatched lines — Herring concentrations.

by echo survey (and supplemented by statistics of catches, in Surveys 5 and 6 only, when large concentrations of herring were located by fishermen beyond the edge of the echo survey).

It will be observed that there is a rough fit, the herring tending to lie under the warmer surface water. In the period between Surveys 4 and 5 the locus of successful fishing moved rather suddenly some 30 miles to the eastward, and we associate this tentatively with the appearance of relatively high surface temperatures offshore. There seems to be no doubt that this sudden rise in temperature is due to an incursion of very warm water on the surface, and in fact there was under this influx a reduction in salinity suggesting an outflow of the colder inshore water beneath.

Late in the season the relatively fresh Moray Firth surface outflow became very warm, but there is no evidence of herring being found under it.

Two interesting points may be mentioned. In one example at X (Survey 6), a group of good catches was taken from a position which appears to be characterised by an anticlockwise eddy and was consequently *cold* in relation to its surroundings. At Y (Survey 9) an exceedingly heavy group of traces, and an isolated group of heavy catches, were taken on the edge of another anticlockwise eddy, and one which is a marked feature of this area in the latter part of the season. The exceptionally heavy concentration obtained here suggests, to me, that this was a concentration working towards an area of low salinity for spawning purposes.

I feel justified in asking the meeting to excuse this somewhat hasty presentation of these results, since they suggest interesting possibilities which, it may be, can be quickly compared with other people's observations and tested against experience in other summer fisheries. The general picture outlined above is of course subject to modification not only in the light of further observations, but also of further detailed study of the present ones, particularly in relation to the plankton sampling which cannot be fully evaluated for some little time.

Reference.

Tait, John B. "Surface Drift-Bottle Results in Relation to Temperature, Salinity and Density Distributions in the Northern North Sea". Rapp. et Proc.-Verb., Vol. 89, Pt. III, Copenhague 1934.

15.

Recent Fishery Hydrographic Results in the United States.

Abstract of paper by

LIONEL A. WALFORD

WITHIN the past three years two fishery hydrographic studies have been started in America, which at once are notable for being the first such undertakings in our part of the world that have been designed and financed to deal effectively with the massive problems they set out to solve.

The first of these is a study of the sardine, which occurs from Baja California northward along the Pacific Coast of America. This fishery has been the object of a large-scale research program since 1947. Several institutions are collaborating in this effort (including those which had been studying the problem for many years previously) to determine how hydrographic conditions control the behaviour, survival, and availability of sardines. Of the results so far attained which are pertinent to the subject of this meeting, the most clear-cut seems to be a demonstration that spawning is confined to water having a temperature range of 12.5° to 16.0° C. The spawning occurs in areas of upwelling, so that these waters are influenced, not only in temperature but in nutrient content, by this phenomenon. There have been two centres of spawning during the past three years—one off southern California, the other off Baja California. These separate spawnings may represent two genetically different stocks of sardines. Spawning begins for both when the water reaches the aforesaid requisite temperature, in general at first in the south and advances northward with the progression of favourable temperatures. The last great year-class (1939) was produced when the spawning area extended hundreds of miles northward beyond its usual range.

The second significant study has developed as a result of the Fish and Wildlife Service establishing a laboratory in Honolulu. This organization has since been conducting a fishery hydrographic study to determine the distribution and abundance of the several species of tunas in time and space. Three research vessels have made systematic hydrographic observations between the Hawaiian Archipelago and 5° South Latitude, and between 172° and 158° West Longitude. In this section, the counterequatorial current was found to lie between 5° and 10° North Latitude. It was found to have a maximum depth of about 200 metres and to flow eastward at a rate of over 2 knots. The north equatorial current (and presumably, the south equatorial current) which flow westerly to either side of the countercurrent, move at a rate of about $^1/_2$ knot or less. Considerable upwelling from depths of about 200 metres was noted during the oceanographic surveys along the equatorial divergence. The result of this upwelling of nutrient-rich water to the surface about the equator, with the resultant lower temperature than in water to the north and south and the higher phosphate content, brings about a more abundant growth of zooplankton than in the adjacent waters. Experimental fishing in this zone has produced much greater catches of tuna than had been taken elsewhere in the mid-Pacific by equivalent gear.

16.

Some Remarks on the German Position in Fishery-Hydrography.

By

G. Böhnecke.

After 1945, the prime requirement of the institutions concerned with fisheries sciences in Germany was the reunion of the people working in the various fields, and the provision of the necessary technical equipment and accomodation most of which had been lost during the war. In "Jahresbericht über die deutsche Fischerei 1950" (Annual Report on German Fisheries 1950) which was recently published by the Federal Ministry of Food, Agriculture and Forestry, A. v. Brandt[1]) gives a good summary of the results of the efforts made and enumerates the ten institutions[3]) which are now dealing partly with the practical side and partly with the scientific side of the problems of the fisheries and/or the hydrography and biology of the sea.

In his article contained in the same report, A. Bückmann[2]) reports on the German Scientific Commission for the Exploration of the Sea which was again convened in 1948, and in which all circles interested in the biology and hydrography of fish are united.

In addition to the above-mentioned organisations, there is an eleventh, the German Hydrographic Institute in Hamburg. This, though its main functions are those of a Hydrographic Office, includes a department of oceanography which not only continues the tradition of the former Deutsche Seewarte, but does work which, it is believed, will also contribute to the solution of questions arising in fisheries sciences. Researches are made on oceanic currents, on marine chemistry (including the content of food stuffs in the sea) and on marine physics, with full attention paid to turbidity and transparency.

Thus, in August 1950, the German Hydrographic Institute investigated the problem of thermoclines in co-operation with the "Institut für Seefischerei", Hamburg, during a cruise of the research and surveying vessel "Gauss" in the northern North Sea. Efforts were made to solve the questions arising in this field by adding to synchronous investigations of temperature, salinity, transparency, turbidity, and of the food stuff and plankton content of the water, attempts to obtain echograms showing the conditions and the reactions of fish at the discontinuity layer. While this first cruise was more one of studying the geographical extension of the thermocline and the phenomena occurring in that layer, plans exist to study (if possible in 1952) the question of the periodical fluctuations of all the factors concerned at a place of marked interest over a longer period.

In order to investigate the resulting water movement in the south-western North Sea (Hoofden) in a way which could be repeated, to throw light on the transport of plaice eggs and larvae, S. S. "Gauss" of the German Hydrographic Institute, working in co-operation with the Kiel "Institut für Meereskunde" in June 1951, laid out 10 recording paddle-wheel current-meters and worked four fairly short current-measuring stations from the anchored ship. The current-meters lay along the two lines: Flamborough Head to "S. 2" L.V. and thence to Texel, and along an east-west section in latitude 52°15′ N., records being taken for about 2 weeks. In conjunction with the records from the continuous current-measurements made with vertical logs from British, Dutch and German light-vessels on the initiative of Dr. Carruthers, the results obtained will provide a synoptic picture of the tidal streams and particularly of the residual currents of this part of the sea. During the period in which the current-meters were laid out, the "Gauss" carried out observations of temperature, salinity, transparency, turbidity, food stuff content and plankton in the area defined. The evaluation of the material is still in progress. Already, however, the connexions between weather conditions (wind) and the residual

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[1]) Dr. A. v. Brandt, Seefischereiforschung. Jahresbericht über die deutsche Fischerei 1950, published by Bundesministerium für Ernährung, Landwirtschaft und Forsten, Berlin 1951.

[2]) Dr. A. Bückmann, Die Arbeiten der Deutschen Wissenschaftlichen Kommission für Meeresforschung. ibid.

[3]) Bundesanstalt für Fischerei
a) Biologische Anstalt Helgoland, Hauptstation List a. Sylt, Abteilung für Fischereiforschung Bremerhaven.
b) Institut für Seefischerei, Hamburg.
c) Institut für Küsten- und Binnen-Fischerei, Hamburg.
d) Institut für Netz- und Materialforschung, Hamburg.
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Institut für Fischereiwissenschaft der Universität Hamburg.
Institut für Meereskunde der Universität Kiel.
Institut für Meeresforschung, Bremerhaven.
Max Planck-Institut für Meeresbiologie, Wilhelmshaven.
Forschungsanstalt für Meeres-Geologie und Meeres-Biologie "Senckenberg", Wilhelmshaven.

currents in this area have been ascertained. Furthermore, all observations clearly showed the predominant influence of the tidal streams in virtually annihilating stratification in this area; there results a strong vertical mixture of the water so that characteristics generally vary only in the horizontal. Between the tongues of Atlantic water coming from the Channel and from the northern North Sea down the east coast of England, there was a tongue of comparatively low salinity (below 34.4 $^0/_{00}$) characterized by a high content of chlorophyll and equally strong turbidity. This tongue commenced in the vicinity of Lowestoft and extended to the north-east. Its chlorophyll traces were observed almost to "S. 2" light-vessel.

The German Hydrographic Institute is particularly grateful that British and Dutch naval craft maintained a regular watch on the marker buoys of the laid-out current-meters, thus probably avoiding major losses of instruments. It is hoped that it will be possible by mutual exchange of observations to increase the value of the material produced by the cruise, and it is intended to repeat the campaign in the spring of 1952 during plaice spawning time (about the end of February and beginning of March).